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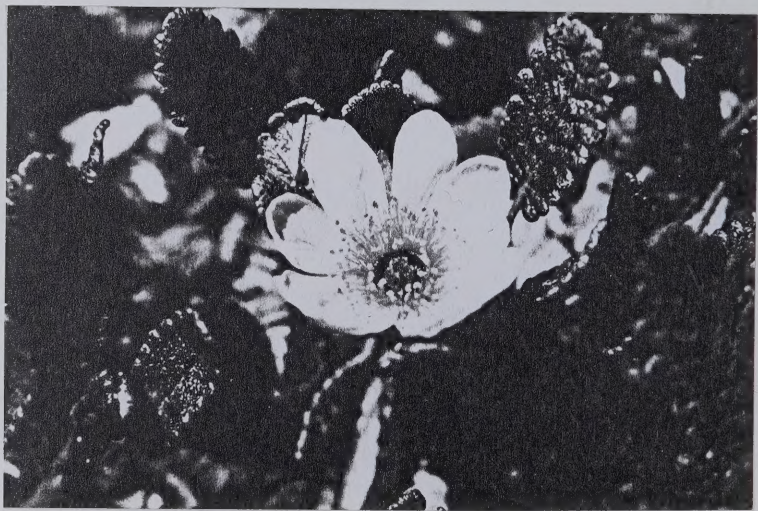

Dryas octopetala L. ssp. *hookeriana* (Juz.) Hulten

THE UNIVERSITY OF ALBERTA

ALPINE TUNDRA COMMUNITIES AND *DRYAS OCTOPETALA* SSP. *HOOKERIANA* IN THE BALD HILLS, JASPER NATIONAL PARK

by

© PETER KUCHAR

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR

THE DEGREE OF DOCTOR OF PHILOSOPHY

IN

PLANT ECOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

SPRING, 1975

on gravelly windswept ridges, and largest in warm sheltered microsites.

There is a commensal relationship between *D. octopetala* and associated biota. Mats in upland tundra often harbor a large assortment of plants and animals. *Dryas* is an ideal host: abundant, stable, long-lived, tolerant of commensals; it is an important source of food (mainly litter), warmth, shelter and stability.

Dryas octopetala is a much better host than mat analogues. *Salix arctica* does not produce a sufficiently coherent mat; *Silene acaulis* is much smaller in size, and covers less area; *Empetrum nigrum* has excessively dense mats, with depauperate arthropod fauna.

A mealybug (*Chorizococcus* sp.) and red spider mite (*Eotetranychus* sp.) were the only important *Dryas* herbivores aside from the numerous pollen and nectar feeders, mainly flies.

Many arthropods seem to prefer the most mesic of microsites in *D. octopetala*/lichen communities. *Dryas* tundra is poor in bugs and beetles but comparable to Heath and Herb Meadows in most other groups.

The outstanding success of *D. octopetala* in the upland alpine habitat of the Bald Hills can be attributed to its relative freedom from diseases and herbivores, its flexible cycle of leaf production, certain physiological adaptations, and the competition-free habitat.

ACKNOWLEDGMENTS

I am grateful to my supervisor, G. H. La Roi, for his advice and patience through the long course of this study, and for his encouragement of its gradually broadening scope.

The cooperation of Jasper Park personnel is deeply appreciated. A special debt of thanks goes to S.M. (Mac) Elder, Maligne Warden during the course of the study. He provided critical logistic support, and proved a ready source of information on the Maligne area. Also helpful in this regard were Gene Shiel, Bob Marak, and Roy Isakson. These fire lookout personnel stationed at the Bald Hills lookout were companionable and informative, and provided many fine cups of coffee. Also helpful in various ways were Dave Pick, former Chief Park Naturalist, and Hans Pfizener, Alpine Specialist.

Excellent field assistance was provided by Eric Stephanson in 1968, Peter Gresshoff in 1969, and Gerald Bonnema for part of the 1970 season as well as some winter trips. Short-term field assistance was given by D. Bedry, P.D. Lulman, K.L. Bell, and by my brothers Len and Paul. The last two, and my sister Kathie, helped in data reduction and some figure preparation.

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I am indebted to the following for insect determinations: S. Allyson (LEPIDOPTERA), J.R. Barron (HYMENOPTERA: Ichneumonidae), E.C. Becker (NEUROPTERA; COLEOPTERA), J. Belicek (COLEOPTERA: Coccinellidae), C.D. Bird (LEPIDOPTERA: Rhopalocera), H.E. Bisdee (HYMENOPTERA: Braconidae), D.E. Bright (COLEOPTERA: Chrysomelidae), D.J.E. Brown (HEMIPTERA), J.M. Campbell (COLEOPTERA: Byrrhidae, Leiodidae, Meloidae, Staphylinidae), B. Cooper (DIPTERA: Agromyzidae, Calliphoridae, Sarcophagidae), R. de Ruette (COLEOPTERA: Carabidae, Cerambycidae, Chrysomelidae, Coccinellidae), L. Forster (DIPTERA: Culicidae), G. Gibson (HYMENOPTERA: Tenthredinidae), G.C.D. Griffiths (DIPTERA: Agromyzidae), K.A. Hamilton (HOMOPTERA: Cicadellidae), B.S. Heming (THYSANOPTERA), H. Howden (COLEOPTERA: Nitidulidae), M. Ivanochko (HYMENOPTERA: Ichneumonoidea, Formicidae, Vespidae), D. Kavanaugh (COLEOPTERA: Carabidae), L.A. Kelton (HEMIPTERA: Miridae), D.J. Larson (COLEOPTERA: Dytiscidae), G. Lewis (LEPIDOPTERA: Nepticulidae), J.E.H. Martin (PLECOPTERA; NEUROPTERA), L. Masner (HYMENOPTERA: Proctotrupoidea), W.R.M. Mason (HYMENOPTERA: Ichneumonoidea), J.F. McAlpine (DIPTERA: Anthomyiidae, Nymphomyiidae, Piophilidae), W.C. McGuffin (LEPIDOPTERA: Geometridae), J. McNamara (COLEOPTERA: Cantharidae, Cerambycidae, Coccinellidae, Scarabaeidae),

M. Meinander (NEUROPTERA: Coniopterygidae), H.E. Milliron (HYMENOPTERA: Apoidea, Symphyta), D.R. Oliver (DIPTERA: Chironomidae), B.V. Peterson (DIPTERA: Bibionidae, Phoridae, Sciaridae, Simuliidae, Therevidae), D. Pforr (LEPIDOPTERA), W.R. Richards (COLLEMBOLA; HOMOPTERA), F. Schmid (EPHEMEROPTERA; TRICHOPTERA), G.E. Shewell (DIPTERA: Ephydridae), A. Smetana (COLEOPTERA: Carabidae, Scarabaeidae, Staphylinidae), H.J. Teskey (DIPTERA: Empididae, Rhagionidae, Sphaeroceridae, Tabanidae, Tipulidae, Trichoceridae), V.R. Vickery (ORTHOPTERA: Acrididae), J.R. Vockeroth (DIPTERA: Anthomyiidae, Dryomyzidae, Mycetophilidae, Scatophagidae, Syrphidae), H.C.W. Walther (DIPTERA: Anthomyiidae, Syrphidae), H.R. Wong (HYMENOPTERA: Tenthredinidae), D.M. Wood (DIPTERA: Anthomyiidae, Culicidae, Tachinidae), C.M. Yoshimoto (HYMENOPTERA: Chalcidoidea).

Other arthropods were identified by R.E. Leech (ARANEIDA), E.E. Lindquist (ACARINA), W.A. Shear (DIPLOPODA; PHALANGIDA), A.A. Weaver (CHILOPODA). For identifications in other animal groups I thank R.S. Anderson *(Diaptomus)* and A. Martell *(Sorex)*.

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1. INTRODUCTION

At the inception of this study, only one in-depth analysis of alpine vegetation anywhere in the Canadian Rockies (Far-Northern Rockies *sensu* Daubenmire 1943) had been completed (Beder 1967). At the time of writing, five additional studies are available (Bryant and Scheinberg 1970, Hrapko 1970, Baig 1972, Trottier 1972, Broad 1973). This is a rather small output for such a large region. Practically any vegetational study here is bound to add considerably to our understanding of these vast alpine areas.

Some important studies of alpine vegetation are available from the U.S. Rocky Mountains (Cox 1933, Bliss 1956, Billings and Bliss 1959, Billings and Mooney 1959, Johnson and Billings 1962, Choate and Habeck 1967, Kiener 1967, Bamberg and Major 1968). Major studies have also been completed in other western mountain ranges (Klikoff 1965, Moore 1965, Johnson 1970, Kuramoto and Bliss 1970, Eady 1971, Chabot and Billings 1972). However, most of the plant communities in these areas are floristically unlike those of the Canadian Rockies. Southward, summer drought conditions (Major and Bamberg 1967), and coastward the much deeper snowpacks, as well as the geographical and geomorphological settings, present environments unlike those in the Canadian Rockies.

Alpine tundra vegetation of Jasper National Park is agreeably close in structure and composition to arctic vegetation. Numerous plant synecological studies are available

from arctic North America (e.g. Hanson 1953, Britton 1966, Barrett 1972, Corns 1974), northern Europe (e.g. Gelting 1955, Nordhagen 1955, Gjaerevoll and Bringer 1965, Raup 1969) and Asia (e.g. Aleksandrova 1960). There are some important environmental differences between arctic and alpine tundra (Bliss 1956), but many species of plants have successfully overcome them.

In the alpine tundra of the Canadian Rockies, as in many parts of the Arctic, *Dryas* is a prominent taxon. It has figured in some northern European vegetation studies (Gelting 1955, Nordhagen 1955, Rønning 1965), but its "builder" aspect (*sensu* Sukachev 1926) and adaptations to environment have gone relatively unheralded. Only recently, in the High Arctic, has it received autecological attention (Mayo et al. 1973, Svoboda 1974).

Since *Dryas octopetala* provided a great deal of the plant cover and biomass of upland tundra in the Bald Hills, it was logical to suppose that it had some effect on associated plant and animal life. A key aspect of the project was the establishment of a solid vegetational base. Too many zoologists ignore or much underestimate the importance of vegetation in the control of animal distribution and abundance. Even Mani (1962, 1968), in his otherwise excellent reviews of insect life in alpine regions, attaches very little importance to vegetation, barely mentioning it. His thesis, that microenvironment governs insect distribution and activity, is correct as far as it goes, but does not acknowledge that in

many alpine situations microenvironment itself is molded by vegetation. Part of the problem is that animal ecologists have traditionally thought "population" rather than "community" or "ecosystem".

The study of alpine invertebrates has been grossly nelgected in North America. The primary reasons for this are lack of interest (or funding), and an unfavorable ratio of numbers of investigators to numbers of species of insects. Aside from superficial studies of windborne insects collected on snow (Caudell 1902, Howard 1918, Van Dyke 1919, Chapman 1954a,b), the only reasonably detailed investigations are those of Hayward (1952) in Utah and Schmoller (1971a,b,c) in Colorado. One other study is presently being completed in the Sierra Nevada by Papp (J.K. Ryan *pers. comm.*).

We are still at level *alpha* with alpine insects and other invertebrates: not only are distributional patterns and ecological relationships very imperfectly known, many of the species have not yet been described. This creates obvious difficulties for one who would study them in a general way. Taxonomic studies (e.g. Nimmo 1971, Griffiths 1972a,b) may include some alpine forms, but there is no emphasis or special consideration of the alpine environment and fauna.

So far the Arctic has been a much richer source of entomological information, due to three large-scale programs:

1) A major study of Canadian subarctic and arctic insects undertaken by the Canadian Department of Agriculture in collaboration with the Canadian Department of National

Defence (Freeman 1958). Much of the work has been at Lake Hazen on Ellesmere Island (Oliver et al. 1964, Leech 1966, Hocking 1968, Kevan 1970).

2) An IBP study at Barrow, Alaska (Bohnsack 1968, Challet and Bohnsack 1968, MacLean and Pitelka 1971, Edwards 1971).

3) An IBP study at Devon Island (Ryan 1972).

Some other areas in the Canadian Arctic Archipelago have been covered (Bruggemann 1958, McAlpine 1964), and studies have been made in North European areas (Hammer 1944, Holm 1950, 1967, Dalenius 1962, Agrell 1963, Lindroth 1965, Solhöy 1972).

2. OBJECTIVES OF STUDY

In its original form, this study had two interrelated objectives: describe the plant communities of the Bald Hills and relate them to environment. As I came to realize the importance of *Dryas octopetala*, I added a number of objectives to the study, all devolving from *Dryas*' primary role in the ecosystem.

The major objectives of this study have been to:

1) Describe qualitatively and quantitatively the floristic composition, structure, phenology, physical habitats and relative abundance of the alpine and forest-tundra plant communities of the Bald Hills, Jasper National Park.
2) Relate plant community patterns to major environmental variables.
3) Prepare a classification of the Bald Hills vegetation.
4) Describe the growth and development of *Dryas octopetala* ssp. *hookeriana*, and some of its adaptations and responses to environment in the Bald Hills.
5) Indicate some interrelationships of *D. octopetala* with associated plant and animal life, and prepare a preliminary checklist of the arthropod fauna of the study area.

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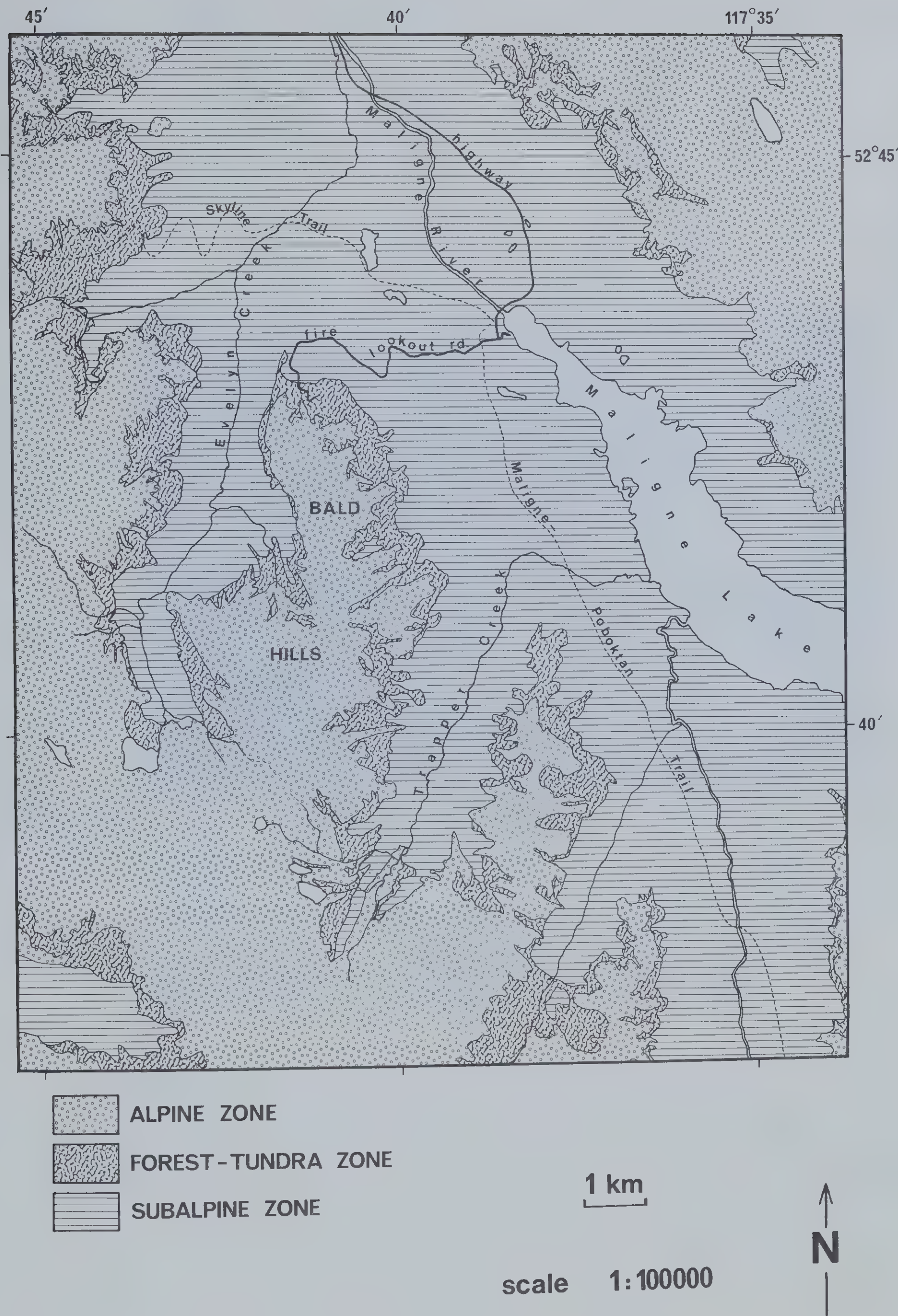

FIG. 1. The Bald Hills and surrounding region.

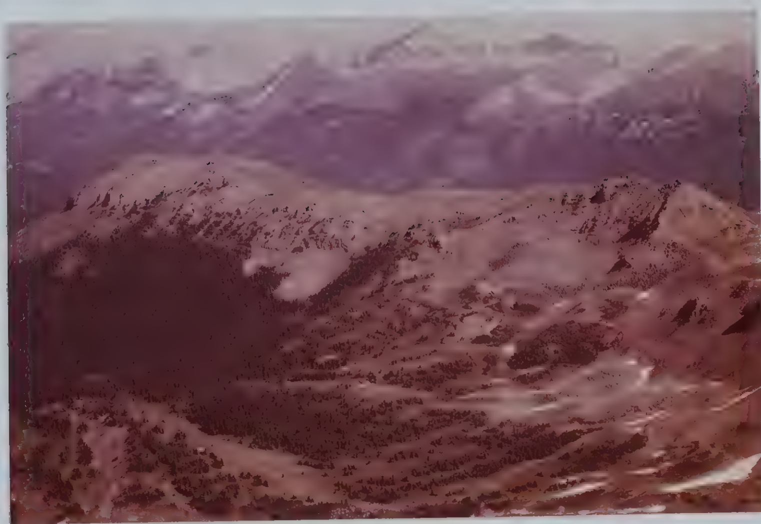

PLATE 2. West side of the northern half of the Bald Hills, photographed 9 August 1968. The steep, unstable upper slopes have negligible plant cover, but the forest-tundra zone has good cover of heaths (green between trees). Note fire line at extreme left-centre. Queen Elizabeth Ranges in background.

Hill was utilized for gravel, and presently the short spur road is actively eroding.

The possibility of former Amerind use is slight - most Indian activity was limited to trapping along Maligne Lake (Schaffer 1912). The Bald Hills have potential as a skiing area, but this has not been exploited except by occasional ski-touring parties (e.g. Stewart 1965). Trails in the area are undoubtedly natural game trails. A former riding concession at Maligne Lake, as well as occasional warden tours by horse, probably had no impact on the area.

Visitor use in the Maligne area as elsewhere in the Rockies has gone up drastically in the last few years, but human impact on the Bald Hills tundra does not appear to be increasing significantly. Perhaps the best evidence for lack of anthropogenic influence is the small groups of Rocky Mountain caribou, an animal truly shunning man, that may be seen in the area practically any time of year including summer.

CLIMATE

The Maligne area has a modified continental climate. Winters are cold, but weather from the Pacific Coast has a moderating influence. The mean annual temperature at Maligne Lake (1675 m) is -1.7°C compared to 2.5°C for Jasper townsite, 665 m lower in elevation. Most of the year the difference is in the order of 5°C, narrowing to about 2°C for November and December. This is not quite the difference that Rawson (1942)

expected when, using adiabatic lapse rate values, he estimated the mean annual temperature at Maligne Lake as -6.0°C. Summers in the Maligne area are fairly cool, and frost is possible any time of year (Parks Canada, unpubl. data).

No year-round temperature data are available for the Bald Hills. Summer temperatures are ca. 4°C lower than at lake-level, an elevational difference of 500 m. Mean minima are about the same, but maxima are consistently greater at lake-level.

The amplitude of diurnal and annual temperatures, as Hrapko (1970) also found at Signal Mountain, is smaller at the higher elevations. In daytime, air at the tops of the mountains and high hills does not warm up as much as at lower elevations. At night cold air drains off the hills, collecting in the valleys and smaller frost pockets. In 1970 for example, the top of the Bald Hills got no colder than -27°C, whereas temperatures of -40°C were recorded at Maligne Lake. Conversely, the hottest day of the year had 21°C in the Bald Hills but 30°C by the lake.

Precipitation in the Maligne area is not high, at 400 mm/yr just slightly higher than the 375 mm at Jasper townsite. About 70% of the precipitation is in the form of snow, progressively more with increasing elevation (Table 1). Summer (July + August) precipitation in the Bald Hills averages 136 mm, but the total varies widely from year to year (Table 2). The summer mean at Benthoud Pass, Colorado is 138 mm (Judson 1965), yet the Colorado Rockies are considered to

TABLE 1. Depth of snow (cm) on ground in Maligne Valley Region[1]. All figures are means for late in each month.

	Medicine L. 1350 m	Maligne L. 1650 m	Bald Hills 1950 m	Bald Hills 2100 m
September	0	0	10	10
October	5	5	10	20
November	25	25	35	45
December	40	45	60	80
January	60	75	90	110
February	65	80	100	120
March	70	85	110	140
April	-	60	85	105
May	0	0-20?	-	60?

[1]Based on records from November 1968 - March 1972 (Parks Canada, unpubl. data).

TABLE 2. Summer precipitation (mm) at the Bald Hills fire lookout.

YEAR	JULY	AUGUST	TOTAL
1963	72	37	109
1964	36	41	77
1965	82	76	158
1966	121	87	208
1967	74	31	105
1968	61	78	139
1969	79	131	210
1970	48	30	78
Mean	72	64	136

have a relatively xeric alpine environment (Major and Bamberg 1967). The Maligne area is definitely not a high snowfall region compared to mountain areas along and west of the Continental Divide.

Prevailing winds in the Bald Hills are from the NW through SW. Winds up to 11 m/sec are not uncommon but speeds of 20 m/sec are very rare. This is in contrast to alpine areas in western U.S., Europe, Asia, and New Zealand where much higher windspeeds have been recorded in steady blows as well as gusts (Judson 1965, Bliss 1969).

Average sky conditions (Table 3) give some idea of the variability in climatic conditions. There are very few totally clear or totally cloudy days. There is a slight daily trend toward greater cloudiness and higher windspeeds (Tables 4,5). In the Colorado Front Range, Clark and Peterson (1967) noted, on the average, slightly more cloud in P.M. than A.M.

Table 3. Daytime sky conditions in the Bald Hills, as percent cloud cover.[1]

YEAR	JUNE			JULY				AUGUST				SEPTEMBER				JULY MEAN	AUG. MEAN	J+A MEAN	No. totally clear days			No. totally cloudy days		
	16	23	30	7	14	21	28	4	11	18	25	1	8	15	22				J	A	J+A	J	A	J+A
1960							37	59	33	58	69	57							-	4	-	-	4	-
1961		34	61	40	44	77	64	33	34	53	18	68				56	43	48	1	6	7	2	2	4
1962					69	79	28	45	69	51	75	79				59	69	62	1	0	1	4	4	8
1963	43	64	75	36	72	71	64	50	41	49	74	37	47	48		61	50	55	0	1	1	2	1	3
1964				49	41	66	59	80	55	57	47	80	55	39	82	54	60	57	0	1	1	1	4	5
1965			78	58	78	65	54	34	50	65	53	58	55			64	57	57	1	0	1	4	3	7
1966		58	68	68	60	61	78	43	75	82	14	65	42	37	34	67	59	61	0	6	6	3	4	7
1967					49	60	51	48	54	15	44	18	56	54	35	53	33	42	0	4	4	1	0	1
1968				18	76	80	52	51	57	88	91	59				57	74	64	2	0	2	4	9	13
1969	44	86	82	75	79	50	78	54	79	64	39	59	64	50	84	71	60	64	0	1	1	8	1	9
1970		38	75	43	30	60	83	61	53	62	26	71	86	58	80	54	53	54	0	5	5	3	2	5

[1] Based on four daily observations (0800, 1100, 1400, 1700 hrs) of each of the sky quadrants from the fire lookout. The dates subtend the preceding week's means. (Parks Canada, unpubl. data)

TABLE 4. Mean monthly cloudiness[1] at four times of day, at the Bald Hills fire lookout, 1961-72.

YEAR	JULY				AUGUST			
	0800	1100	1400	1700	0800	1100	1400	1700
1961	44	55	62	67	35	42	48	48
1962	61	65	64	64	62	66	73	73
1963	59	56	69	59	45	48	52	56
1964	51	54	56	56	54	60	62	63
1965	50	66	69	70	54	59	55	58
1966	59	69	72	69	60	60	60	57
1967	55	65	65	64	23	36	36	40
1968	52	52	63	59	70	72	73	72
1969	59	72	70	75	54	62	59	66
1970	47	49	56	63	51	52	55	53
1972	63	69	69	76	31	40	50	55
MEAN	55	61	65	65	49	54	60	58

[1]Percent cloud cover, based on daily observations of each sky quadrant. (Parks Canada, unpubl. data).

TABLE 5. Mean monthly windspeed[1] at four times of day, at the Bald Hills fire lookout, 1961-68.

YEAR	JULY				AUGUST			
	0800	1100	1400	1700	0800	1100	1400	1700
1961	0.8	0.9	1.1	1.1	0.7	1.2	1.3	1.2
1962	0.9	1.0	1.1	1.1	0.8	1.2	1.4	1.4
1963	1.1	1.2	1.5	1.5	0.7	1.0	1.1	1.2
1964	1.0	1.1	1.4	1.3	1.0	1.2	1.5	1.4
1965	0.8	1.1	1.3	1.9	0.6	0.9	1.3	1.5
1966	1.0	1.1	1.2	1.2	1.0	1.0	1.3	1.2
1967	0.9	1.1	1.3	1.4	0.7	1.1	1.3	1.5
1968	1.0	1.1	1.3	1.4	0.9	1.1	1.2	1.3
MEAN	0.9	1.1	1.3	1.3	0.7	1.1	1.3	1.3

[1]On a relative scale: 1=light, 2=medium, 3=strong. (Parks Canada, unpubl. data).

Mean monthly cloud cover is 58%, but can vary a lot, especially in August. The weather in the Bald Hills and Maligne area in general is rather unpredictable, both within a given season and from year to year.

PHYSIOGRAPHY AND GEOLOGY

The Bald Hills comprise a series of large rounded hills or small mountains trending N-S along the west side of the Maligne Valley. They form one of a number of eastern outliers of the Maligne Range, connected only at the southern end (Fig. 1). It may be instructive to view them as a peninsula of alpine tundra jutting northward into a sea of subalpine forest, and adjoining an extensive and very rugged alpine area (Mt. Kerkeslin and Endless Chain Ridge).

The Bald Hills lie at the extreme eastern edge of the Main Ranges of the Rocky Mountain Cordillera. The Pyramid Fault, the dividing line between the Main Ranges and Front Ranges, runs N-S between the Bald Hills and Maligne Lake. East of the lake are the Queen Elizabeth Ranges, primarily Devonian and Carboniferous limestones and dolomites of extreme relief (Mountjoy 1964). North-northwest of the Bald Hills are outliers of the Maligne Range, chiefly Precambrian quartzites. Southeast are further outliers, then large mountains (e.g. Mt. Unwin, Llysfran Peak) of Cambrian and Ordovician sediments. West and S of the Bald Hills lies the main mass of Maligne Range. Local relief is 1500 m.

The Bald Hills are composed of Upper Cambrian and Lower Ordovician sediments, mainly shales and conglomerates. Detailed studies of bedrock geology here or elsewhere in the Maligne area are lacking. The area is included on a small-scale map by Price and Mountjoy (1970) that covers the southern half of Jasper Park. The surficial geology of the Maligne Valley has been mapped by Roed (1964) but the Bald Hills were not included. The hills owe their rounded shapes to the scouring action of Pleistocene glaciers which may have reached 2400-2500 m in this area. Thus the top of Hipeak[1] (Fig. 2) was not overridden, but glacial events played a preeminent role elsewhere.

In the northern part of the Hills, the E side has a rolling, somewhat irregular terrain of thin till, colluvial slopes and bedrock exposures, leading eastward into a ridge and gully topography at around timberline. East-centrally, a small cirque glacier produced a cliff, a mass of boulder debris, and two sizeable E-trending ridges. The W side of the Hills is very steep, a series of cliffs and ridges above thinly vegetated talus and forested colluvium. The high slope angle is probably the result of undercutting by a glacier originating at the base of Hipeak. This cirque glacier produced the 300 m high N face of Hipeak, the boulder field at its base, and the flanking moraines.

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[1]Unnamed mountain centrally located in the Bald Hills.

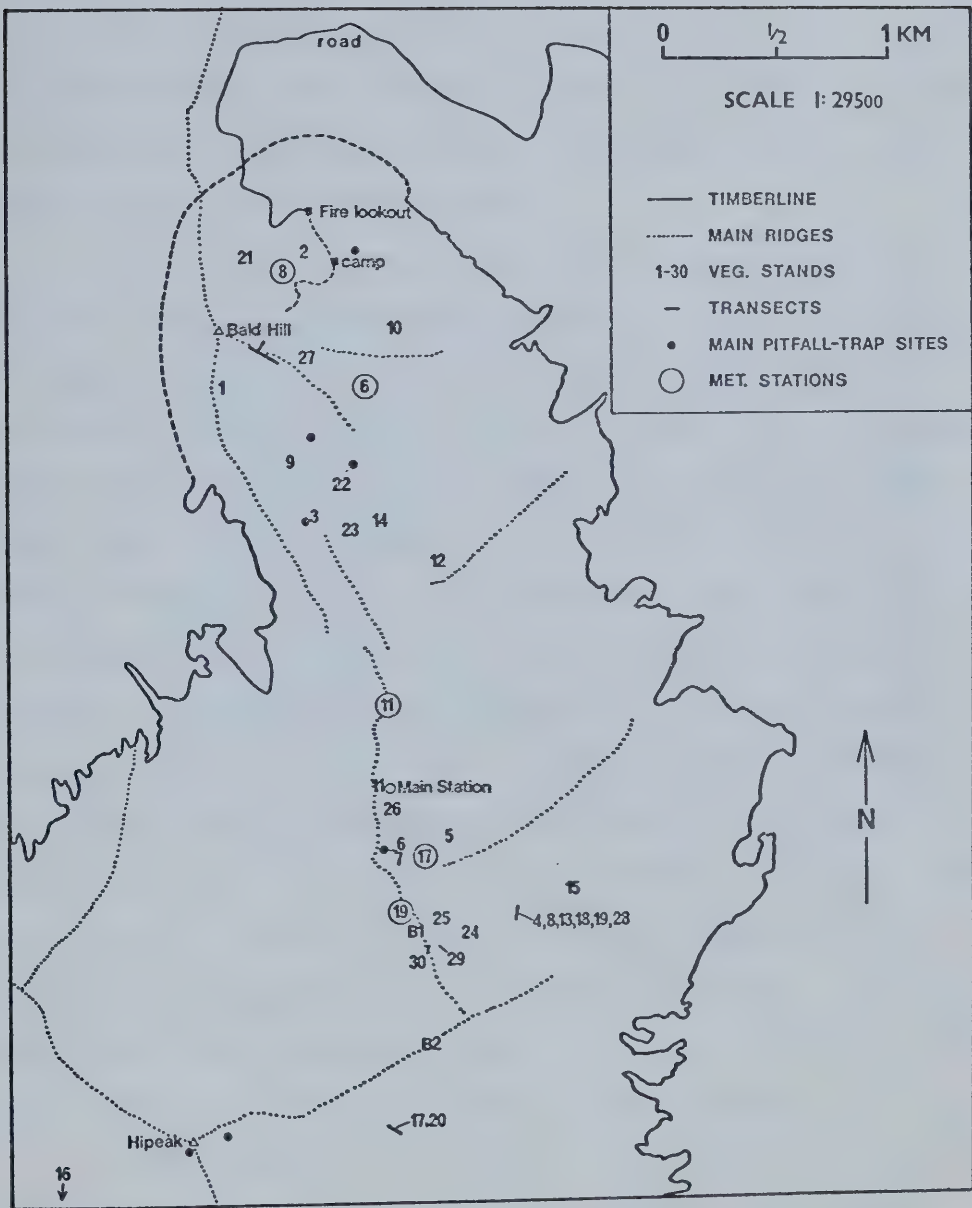

FIG. 2. Major sites of study in the Bald Hills.

In the southern part of the Hills the physiography is reversed. The W side comprises a 4x1 km hillside, its till-mantled lower slopes dissected by recent water erosion into shallow gullies. The E side includes a long series of cliffs 100-200 m high, with an apron of flat alpine terrain and ridge and gully topography eastward.

Today there are no glaciers or nivation hollows in the Bald Hills, but neighboring ranges hold alpine glaciers and small icecaps up to 20 km^2 in area. A wide array of periglacial features (e.g. Plate 3) can be found in the Bald Hills: turf hummocks; circles, polygons, nets and stripes; large stone stripes; fields of solifluction terracettes and smaller numbers of sizeable solifluction lobes; debris islands in boulder fields. Permafrost has been reported in the Rocky Mountains (Johnson and Billings 1962, Ogilvie and Baptie 1967, Ives and Fahey 1971) but I did not find any in the study area. In addition to its preeminent role in patterned ground development, ice is also involved in frost wedging, the chief weathering process in the Bald Hills. Of lesser importance are granular disintegration and cavernous weathering. Also at work is mass displacement through occasional rock falls, small rock slides, and downslope creep of talus fields.

The physiography of the Bald Hills has had an important influence on plant colonization and community development. In the northern half, where I did most of my work, S-facing communities are uncommon and W-facing communities virtually non-existent due to the coarse, unstable and dry surfaces.

PLATE 3. Intense frost action has prevented plant establishment on these sorted polygons, whereas surrounding forb meadows have a rich bryophyte and vascular plant cover.

Most of the vegetated terrain is of two types: (1) ridges and small plateaux where xeric fellfield and other rock-based communities have developed, and (2) N and E-facing slopes, cooler and less dry, with a solid heath mantle. Meadows are small and local. There are also a few small ponds above timberline.

SOILS

Some studies have been made of alpine soils in North America (e.g. Retzer 1956, Nimlos and McConnell 1962,1965, Sneddon et al. 1972a,b, Knapik 1973, Knapik et al. 1973). Alpine tundra soils typically have very shallow profiles, poorly developed horizons, weak to nonexistent structure, low clay content, a high degree of soil instability largely due to frost action, high content of weakly decomposed organic matter in the surface horizons, and limited diversity of types. Significant amounts of amorphous aluminum and iron compounds may be present (Knapik et al. 1973). Knapik (1973) noted that "classification of alpine soils is very confusing due to the many systems that have been used as well as the general lack of information on alpine soils."

Tundra soils in the Bald Hills as elsewhere belong to three orders: 1) Brunisols, 2) Gleysols and 3) Regosols. The best development in alpine tundra soils is exhibited by brunisols. Alpine Dystric Brunisols have been characterized by Knapik et al. (1973) as turfy alpine soils, strongly acid,

with brownish sola and low base status, and without eluviated horizons. Coarse rock fragments are common in most profiles, and increase with depth. Most soils of this type have developed on glacial till, under heath vegetation. In limestone ranges Alpine Eutric Brunisols develop. These are very calcareous, base-saturated, with black Ah horizons. Where the B horizon is weakly developed, profiles are characterized as Lithic Brunisols.

In sites of impeded drainage gleysols may develop. Where plant cover is sparse, the organic matter content is low and soils here are characterized as Orthic or Rego Gleysols. Under good plant cover and 10-15 cm accumulation of organic matter, Humic Gleysols develop (Knapik et al. 1973).

Soils with horizon development too weak to meet the requirements of any order are by default regosols. In many alpine sites pedogenic development is minimal, and accumulation of organic matter only immediately beneath plants. Orthic Regosols characterize fairly stable sites with very simple profiles of rocks, pebbles and fines that show very little change with depth. Cumulic Regosol profiles are found on some steep slopes where the soil pedons have been churned up by gravitational movement (Knapik et al. 1973).

Soil under tree islands in the forest-tundra zone (see below), and in continuous forest below timberline, has a profile quite distinct from tundra soils. There is a characteristic eluvial A horizon and illuvial B horizon. The Canadian system of soil classification (Can. Dept. Agr. 1974) would

place these in the Luvisolic order.

VEGETATIONAL ZONATION

Altitudinal zonation of vegetation has a long history of investigation, and a number of different systems of terminology have been advocated (Daubenmire 1943, Löve 1970).

In my own study, "subalpine" refers to higher-elevation continuous forest dominated in the climax condition by *Picea engelmannii* and *Abies lasiocarpa*. This has been the traditional use of the term in Jasper N.P. (e.g. Heusser 1956, Beil 1966), and in other parts of the Rocky Mountains (Daubenmire 1943, Oosting and Reed 1952). Above timberline, which delimits the upper edge of the subalpine zone, forest gives way gradually or rather suddenly to a tundra landscape where low (<0.5 m high) vegetation predominates (Plate 4).

The commonly used term "treeline" purports to delimit a purely tundra landscape from the last of erect coniferous growth. However, the term has very limited use. Above timberline, scattered conifer islands grade into krummholz on exposed ridges. The belt is not at all uniform-width (cf. Fig. 1). Forest islands and tundra interfinger, and a continuous upper line is not delineable. "Alpine" is the "zone in which tree species can no longer maintain upright, supranival flagging" (Hrapko 1970). However, local wind conditions rather than altitude-related factors constitute the most important shaping influence on conifer form at these elevations.

PLATE 4. East side of the Bald Hills, looking south. Predominant cover is heaths, also some krummholz and tree islands of *Abies lasiocarpa*. The yellow patches are *Carex nigricans* snowbeds; snow covers bare gravel.

Between treeline and timberline is the forest-tundra zone (forest-tundra ecotone of Weaver and Clements (1938), also known as the hudsonian, subalpine, or krummholz zone (Löve 1970)). The term "forest-tundra" is quite unambiguous, referring to a landscape with both forest and tundra elements, viz. moderately low (5-10 m) conifer clumps dotted over a tundra matrix chiefly of heaths (Plates 2,4). Dividing the above-timberline landscape into forest-tundra and alpine sections has ecological merit. For example, a number of mountain birds are restricted to one or the other zone (Kuchar 1972). However, the non-tree vegetation is similar from timberline to well up into alpine. There are probably gradual upslope shifts in composition and dominance, but nothing sudden enough to warrant an alpine-nonalpine distinction. In the present study, therefore, I rely on the descriptive landscape term "tundra" rather than the zonal term "alpine".

As elsewhere in the Maligne Range except the very N end where it seems depressed (Hrapko 1970), timberline in the Bald Hills averages 2040 m on the E side and 2130 m on the W side. The amplitude of timberline is ca. 300 m, from 1925-2225 m.

The landscape at 2040-2200 m is forest-tundra, its upper limit in places reaching 2350 m. Above treeline, conifers are very stunted (krummholz) and give way to a strictly tundra landscape ("alpine"). Its mean lower limit is 2130 m on the E side of the Bald Hills and 2200 m on the W side, but significant areas of tundra can be found down to 2000 m.

At the N end of the study area, particularly its W slope, true timberline cannot be traced with any degree of confidence. A fire in the 1890's swept up to 2100-2200 m, and the slow rate of regeneration combined with erosion have obscured the position of the former timberline (Fig. 2).

FLORA

Vascular plants in the Bald Hills number 197 species in 96 genera and 34 families (Table 6, Appendix 1). Larger

TABLE 6. Numbers of plant and animal taxa seen or collected in the Bald Hills.

PHYLUM/ DIVISION	CLASS	ORDER	FAMILY	GENUS	SPECIES	SPECIES IN PHYLUM /DIVISION
Lichenes	Ascomycetes	2	20	40	135	
	Fungi Imperf.	1	1	1	2	
						137
Bryophyta	Hepaticae	2	11	17	26	
	Sphagna	1	1	1	6	
	Musci	8	23	49	86	
						118
Tracheophyta	Lycopodineae	1	2	2	5	
	Equisetineae	1	1	1	1	
	Filicineae	2	2	4	4	
	Gymnospermae	1	2	4	4	
	Angiospermae					
	Monocots	2	4	17	50	
	Dicots	18	23	68	132	
						196
Arthropoda	Crustacea	1	1	1	1	
	Diplopoda	1	1	1	2	
	Chilopoda	1	1	3	4	
	Insecta	13	94	334	474	
	Arachnida	3	51	111	161	
						642
Chordata	Aves	6	21	47	57	
	Mammalia	5	12	22	27	
						84
(totals)	17	69	271	723	1177	

families include the Compositae (31 species), Gramineae (20), Cyperaceae (23), Cruciferae (13), Rosaceae (11), Saxifragaceae (11), Ericaceae (10), Ranunculaceae (10), and Caryophyllaceae (9). Large or ecologically important genera are *Antennaria, Arnica, Carex, Cassiope, Draba, Dryas, Erigeron, Luzula, Phyllodoce, Poa, Potentilla, Salix,* and *Saxifraga.* The chief growth forms are dwarf shrub, rosette, cushion, and tussock (tuft).

Most of the species also occur in the subalpine zone. Less than 20% seem restricted to above-timberline habitats. These include *Lycopodium alpinum, Luzula arcuata, Carex albonigra, C. glacialis, C. haydeniana, C. incurviformis, C. nardina, C. phaeocephala, C. rupestris, Kobresia bellardii, Agropyron latiglume, Hierochloe alpina, Poa lettermanii, P. rupicola, Cerastium beeringianum, Anemone drummondii, Ranunculus gelidus, Papaver kluanensis, Draba paysonii, Erysimum pallasii, Luetkea pectinata, Potentilla hyparctica, P. nivea, P. uniflora, P. villosa, Oxytropis podocarpa, Cassiope tetragona, Gentiana glauca, Pedicularis arctica, Campanula lasiocarpa, Arnica latifolia* var. *gracilis, A. louiseana, A. rydbergii, Crepis nana, Erigeron humilis, E. pallens, Saussurea densa, Senecio fremontii, Taraxacum lyratum.*

Ca. 10% of the flora comprises subalpine species found very locally and near timberline in the study area. They represent a subalpine element, near its altitudinal limit at timberline. Another 10% of the species were represented by small numbers of individuals at just one or two sites in the

Bald Hills.

Both bryophytes and lichens are exceedingly well represented in the study area, with 118 and 137 species respectively (Table 6). The larger lichen genera, all with eight or more species, include *Cetraria*, *Cladonia*, *Lecanora*, *Lecidea*, and *Peltigera*. By growth form 36% are fruticose, 21% thallose, and 43% crustose of which almost half are saxicolous. Important bryophyte genera are *Bryum*, *Dicranum*, *Polytrichum*, *Rhacomitrium* and *Tortula*. In tundra studies it is unusual to have a complete or near-complete list of bryophytes and lichens such as the one here (Appendix 1), therefore comparisons between different regions are not really possible. It seems, however, that the Bald Hills tundra and other areas in Jasper Park are much richer in cryptogams than the U.S. Rockies e.g. central Montana (Bamberg and Major 1968), but not as diverse as some mountain areas e.g. central Transcaucasus (Major and Bamberg 1967).

Bacteria, algae and fungi were not studied. A preliminary plate-dilution of some surface soil layers revealed a fairly rich bacterial flora, but this was not pursued. Terrestial algae are inconspicuous and uncommon in the Bald Hills. A few of the small waterholes near ponds have algal growths. The phenomenon of red snow, due mainly to *Chlamydomonas nivalis* Wille (Kol 1964), is seen here as in other parts of the Rockies. Tundra fungi may be diverse but are inconspicuous and for the most part microscopic. A sparse scatter of mushrooms on the tundra adds infinitesimally to plant cover.

Small puffballs (*Lycoperdon*) are the commonest.

Nomenclature and taxonomy follow Hitchcock et al. (1955-69) for vascular plants, Crum et al. (1973) for mosses, Isoviita (1966) for sphagna, Frye and Clark (1937-47) and Schuster (1966,1969) for hepatics, and Hale and Culberson (1970) for lichens. Vascular plant exceptions include *Agropyron latiglume*, of the *A. caninum* complex; and *Festuca brachyphylla*, of the *F. ovina* complex. Species not found in Hitchcock et al. (1955-69) were taken from Hulten (1968). The treatment of Mnicaceae follows Koponen (1969), Polytrichaceae follows Smith (1971), and *Lescuraea* follows Lawton (1971).

A set of vouchers of vascular plants. bryophytes and lichens is deposited in the Herbarium of the Department of Botany, University of Alberta (ALTA). Sets of bryophytes and lichens are also deposited in the Herbarium of the Department of Biology, University of Calgary (UAC).

FAUNA

About a thousand species of invertebrates are resident in the Bald Hills tundra. Flies, parasitic hymenopterans, beetles, moths and spiders are the most important macro-invertebrates (Appendix 2). Mites and collembolans are smaller in size and much less conspicuous, but numerically and probably ecologically more important. Major groups of invertebrates that were not sampled include rotifers, nematodes and enchytraeids. Based on diversity estimates in arctic

tundra sites (J.K. Ryan *pers. comm.*), the three groups might embrace 30% of the invertebrate fauna of the Bald Hills.

A total of 84 species of vertebrates have been recorded from the Bald Hills (Appendix 3). Only about 25% are significant elements in the tundra ecosystems here. White-tailed ptarmigan, water pipit, horned lark and gray-crowned rosy finch are the only birds breeding in upland tundra situations in the Bald Hills. Common nesters in the forest-tundra zone and near krummholz patches are the robin, hermit thrush, fox sparrow, Brewer's sparrow, and golden-crowned sparrow. Important herbivorous mammals in the Bald Hills are the pika, Columbian and golden-mantled ground squirrels, Rocky Mountain caribou, mule deer, and some microtines. Mountain goats frequent the southern half of the area. Carnivores include shrews, marten, ermine, wolverine, the occasional grizzly, and the golden eagle. More information on the birds and mammals of the area can be found in Kuchar (1972).

Invertebrate taxonomy follows Borror and DeLong (1964). Nomenclature of Rhopalocera (Lepidoptera) follows dos Passos (1964), and various authorities for other groups. Nomenclature and taxonomy follow American Ornithologists' Union (1957) and Eisenmann et al. (1973) for birds, and Soper (1970) for mammals.

Representatives of most insect, spider and mite taxa are deposited in the Canadian National Collection, Ottawa. Some sawflies are deposited at the Canadian Forestry Laboratory, Edmonton. Centipedes are at Wooster College, Ohio, and

millipedes and phalangids at Concord College, W.Va. Many flies and parasitic hymenopterans remain in my personal collection.

4. PHYSICAL ENVIRONMENT

METHODS

A Main Station was established centrally in the Bald Hills (Fig. 2) on a gently SE-sloping plateau at 2300 m. The vegetation was a mosaic of heath and *Dryas*-dominated communities. Inside a Stevenson screen set on the tundra surface were a Belfort hygrothermograph (sensor 10 cm above ground) and a Moeller distance-recording thermograph with leads at 0, -10 and -30 cm. Both instruments were calibrated at the beginning and end of each season. On the tundra were a three-cup totalizing anemometer (+40 cm) and an actinograph (+10 cm).

A portable station, moved to a new site every two weeks or so, included a hygrothermograph inside a louvered aluminum shelter, and an anemometer. Daily maximum and minimum temperatures at +10 cm were taken through the season at several sites using sixes-type Taylor thermometers mounted under shelters of plywood and styrofoam. Precipitation and wind pattern in a wide range of communities and sites were investigated using ca. 90 1.4 liter (48 oz) tins, aperture diameter 10.5 cm, charged with mineral oil.

Daily means of thermograph data were calculated by averaging hourly values. Comparison of these means with those obtained by simply averaging maximum and minimum showed no significant differences. There was a slight bias toward higher than true mean when max-min average was used, as Bliss (1956) also found.

Over 100 soil profiles were exposed, most to the C

horizon, in a wide range of plant communities. Each horizon was noted and thickness measured. Depth and degree of root penetration, abundance of cobbles, and evidence of congeliturbation were noted. Samples were collected from each horizon, air dried, and the fines fraction sieved out. Texture was determined by the hydrometer method (Bouyoucos 1951). Color of dry samples was determined using Munsell color charts (Anon. 1963). Chemical analysis* was done by the Soils and Feed Testing Laboratory, Univ. Alberta, Edmonton.

Duplicate soil samples at 0-8 and 15-23 cm were taken with a probe sampler, in 15 communities, in early July, August and September 1970. Soil temperatures (-15 cm) were taken at various sites and times with a Weston probe thermometer.

Photographs were taken at ca. weekly intervals from a number of fixed positions, to follow snow release patterns.

On several winter trips in 1969-71 I made general observations on snow accumulation patterns; using a 1.8 m probe, took 2 - 6 measurements of snow depth in a variety of communities; obtained duplicate or triplicate snow density samples from different sites and depths; took some readings of soil, surface, and ambient temperatures.

SUMMER CLIMATIC CONDITIONS

The range of summer weather in the Bald Hills is depicted in Fig. 3. No.1 represents the commonest type of day, with a sunny morning and cloudy afternoon, and fairly light

*N extracted with water and determined by the phenyldisulfonic acid procedure; P extracted with ammonium fluoride and sulfuric acid and determined by the ammonium molybdate vanadate procedure; K extracted with ammonium acetate and determined by flame photometry; pH by a 1:1 soil:water paste with an electrode pH meter.

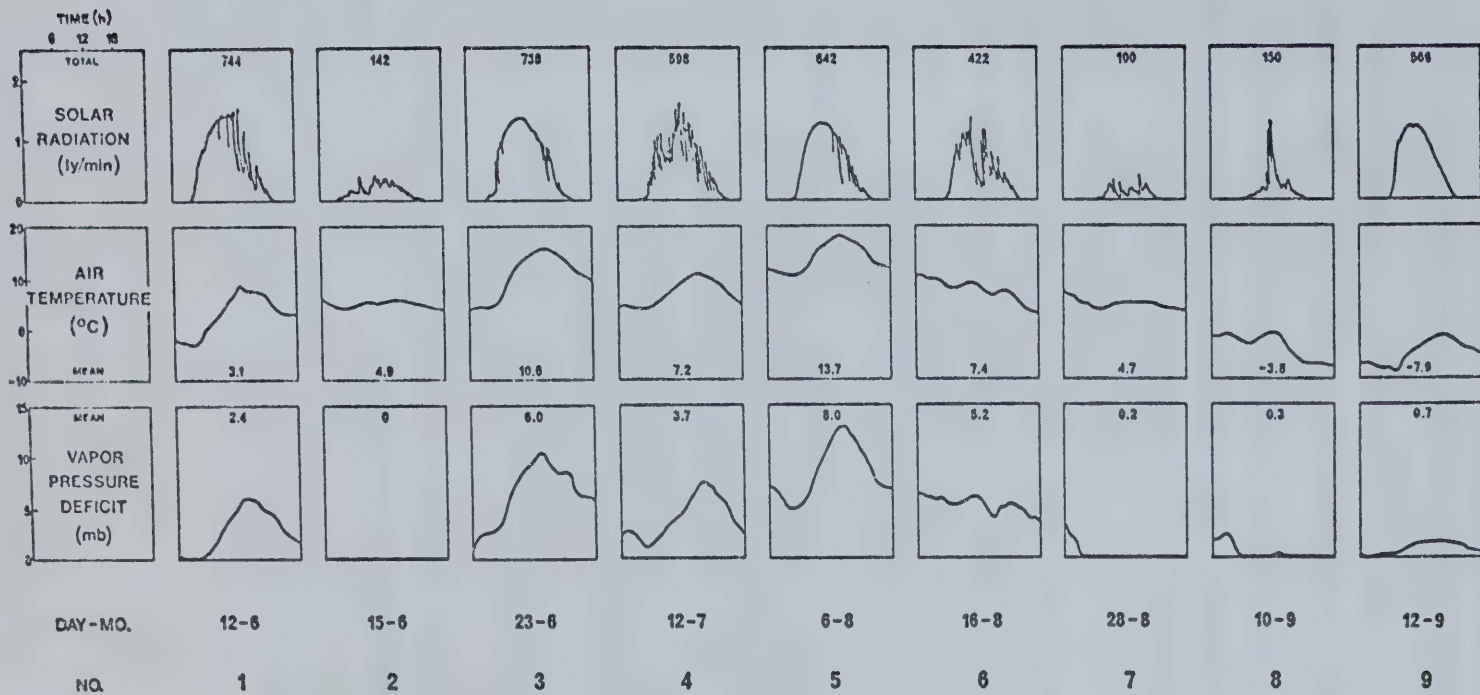

FIG. 3. Weather conditions and vapor pressure deficits for certain days in 1970, Main Station, Bald Hills.

wind. No.4 is also fairly representative. The typical daily trend is one of rapid warming in the morning, and gradual cooling following the early to mid-afternoon peak.

Essentially clear days, all with light wind, are exemplified by no.3, 5 and 9. The first one, early in the season, has higher temperature and VPD than no.9, beyond the end of the growing season of vascular plants. No.5 had the highest mean VPD for the year.

The remaining profiles show abnormal instances of synchronized march of solar radiation, temperature and VPD.

No.2 Fog and rain all day, strong N wind in afternoon. Solar radiation was very low, and VPD zero.

No.6 SE wind from previous day, averaging 10 m/sec by late A.M. This creates anomalous conditions of high temperature and VPD through the night. Sudden shift to N wind in P.M., resulting in temperature drop.

No.7 Low clouds all day, wind nil to very light. Lowest recorded total of solar radiation for the summers of 1968-70.

No.8 Fog and snow flurries in A.M. Sudden strong NW wind in P.M. bringing abrupt temperature drop.

Weather in the Bald Hills is generally unpredictable, and there may be extremes or anomalous conditions of temperature, wind, and cloud cover. However, they do not seem to last long, and the majority of days have the normal warming-cooling trend.

SOLAR RADIATION

Mean daily increment of solar radiation in summer was

437 ly (Table 7). The extremes recorded were 100 ly on 28 Aug 1970, and 793 ly on 19 June 1970. On Signal Mt., Hrapko (1970) reported a mean of 502 ly/day in the summer of 1967, and a range of 198-837 ly/day. Instantaneous values in the Bald Hills did not exceed 1.7 ly/min. These are not high compared to those in some high-mountain areas where the solar constant may be exceeded (Clark and Peterson 1967).

TEMPERATURE

At the Main Station, mean monthly temperature in the

TABLE 7. Summary of July-August, 1968-70, environmental data for the Main Station, Bald Hills.

ENVIRONMENTAL PARAMETERS		1968 J	1968 A	1969 J	1969 A	1970 J	1970 A	SUMMER 1968-1970
Temp. (^{o}C)	mean	7.4	6.6	5.8	6.0	8.7	8.1	7.1
	mean max	9.1	9.1	9.9	9.6	11.9	12.5	10.4
	mean min	3.8	3.7	2.1	2.2	5.2	4.2	3.5
	abs. max	14.0	13.5	15.5	20.5	18.0	18.5	
	abs. min	0.5	0.5	-1.2	-1.0	0	0	
R.H. (%)	mean	72.7	75.5	76.8	71.3	71.3	69.0	72.8
	mean max	91.7	90.5	95.1	91.0	89.1	90.4	91.3
	mean min	55.0	57.4	57.9	55.0	56.9	50.5	55.5
V.P.D. (mb)	mean	3.06	2.54	2.35	3.03	3.52	3.61	3.02
WIND (m/sec)	mean speed at 40 cm	1.77	1.44	1.91	1.97	2.10	2.07	1.88
(mi/hr)	above surface	3.96	3.22	4.26	4.42	4.70	4.65	4.20
SOLAR RADIATION (ly/day)		462	314	472	420	520	432	437
DIURNAL CLOUD COVER* (%)		57	74	71	60	54	53	62
PRECIPITATION* (mm)		61	78	79	131	48	30	142

* At fire lookout.

summer was 7.1°C (Table 7). The seasonal trend of air temperature in 1969 and 1970 is depicted in Fig. 4. No part of the growing season seems distinctive in air temperature regime. Note the sudden drop in early September 1970 (Fig. 4), a graphic depiction of the end of the growing season.

Diurnal trend of air temperature is shown in Fig. 5. Amplitude is much greater at the ground surface than 10 cm above. It is very much dampened at 15 cm in the soil, and virtually nil at 30 cm.

Air temperatures of S and W aspects have relatively high maxima and minima (Fig. 6, Stn 19). Tops of hills and higher ridges (Fig. 6, Stn 11,17) have lower temperature maxima but higher minima. A similar relationship was reported by Hrapko (1970) for Signal Mt., Jasper Park. The lower maxima are due to cooler air at higher elevations; the higher minima indicate the presence of inversion layers. Cold air drains away from the tops into shallow basins and slopes at the foot of the hills (e.g. Stn 6,8).

The relationship of topographic position to night temperatures is evident from Table 8. Many more nights of freezing temperatures were encountered in air-drainage channels (Stn 6,8) than on hilltops (Stn 11,17). Monitored for one month (Aug 1968), the upper N, W and S sides of the Bald Hill had 7-8 frost-nights, but the E side had 13. Heath tundra, intermediate between upland and basin sites, had 15-25% frost-nights.

One microhabitat that often remains frost-free while

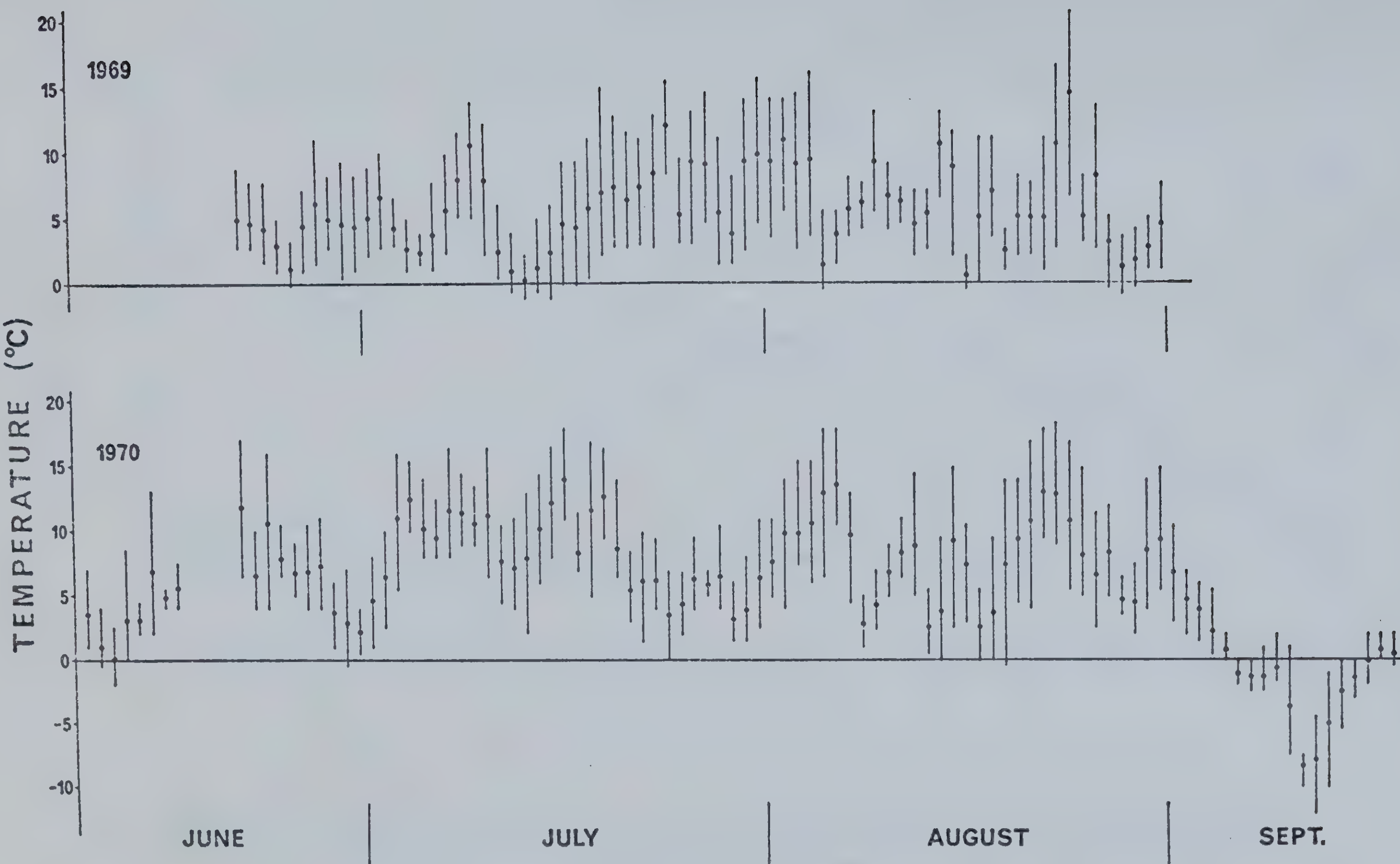

FIG. 4. Seasonal trend of daily mean, maximum and minimum air temperature (+10 cm) at the Main Station, 1969 and 1970 (hygrothermograph data).

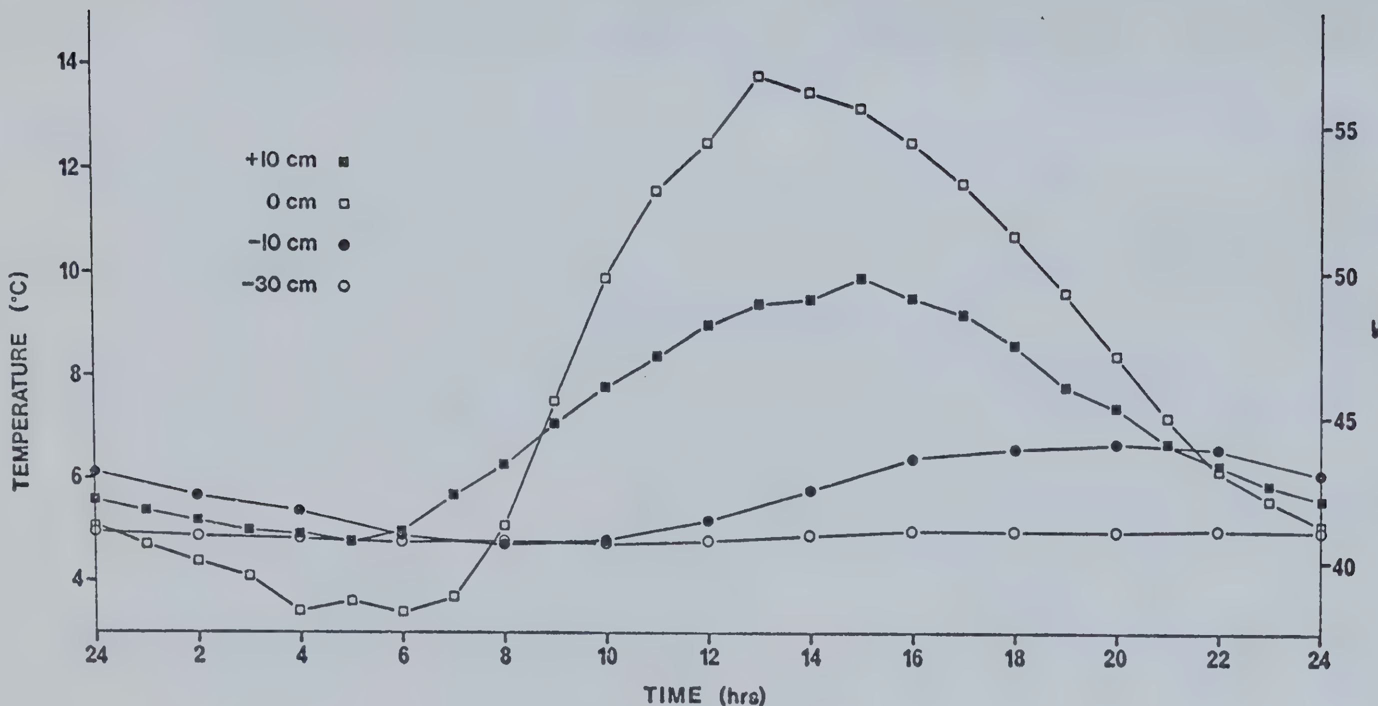

FIG. 5. Daily trend of air and soil temperature at the Main Station. (Hourly means of daily values over July and August 1969).

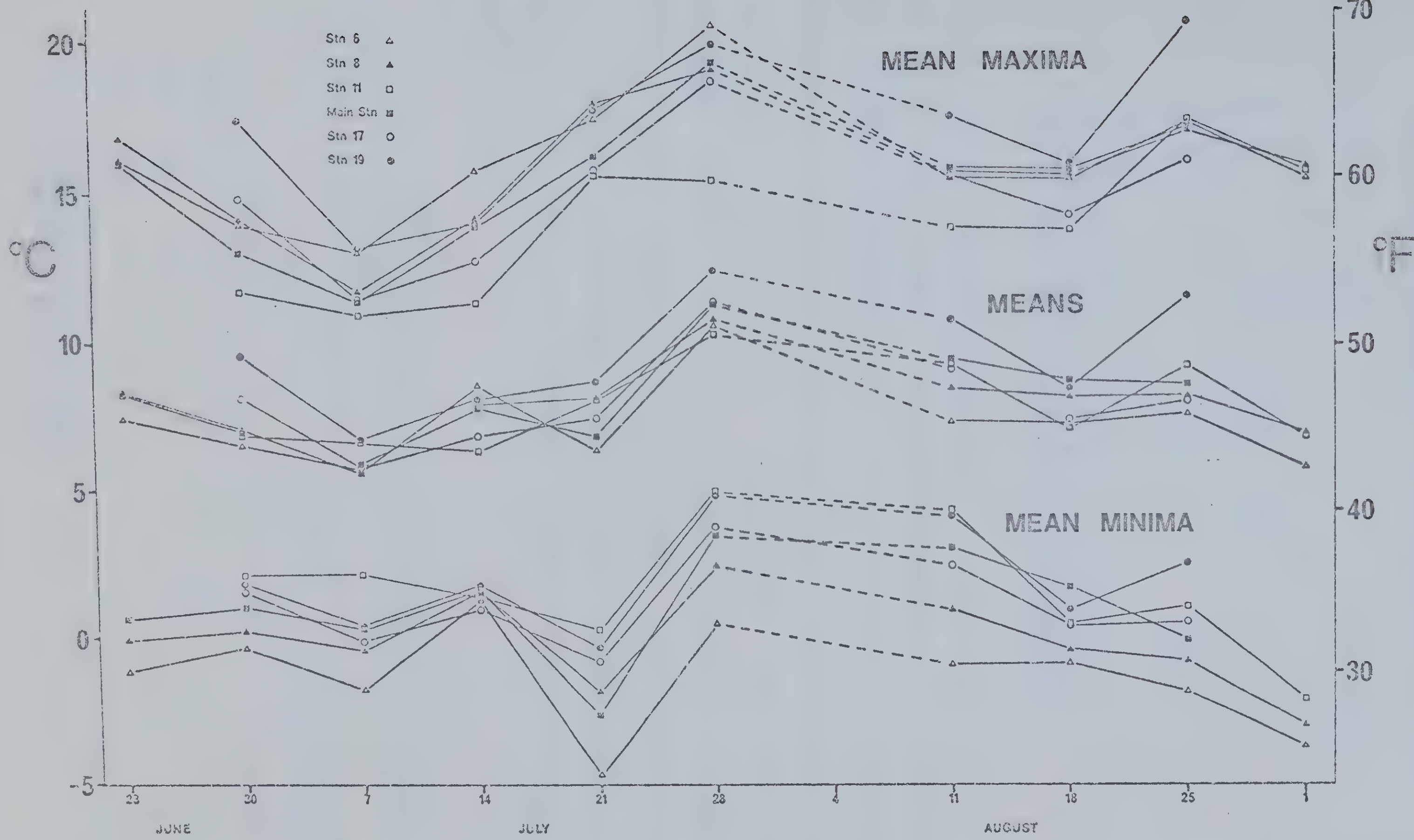

FIG. 6. Weekly mean, mean maximum and mean minimum air temperature (+10 cm) at six sites, 1969.

TABLE 8. Monthly numbers of freeze-thaw cycles at selected stations in the Bald Hills, July & August 1968-70.

Station	1968 J	1968 A	1969 J	1969 A	1970 J	1970 A	Percent of through-freezing days J	A	MEAN
Stn 6		16	17	21	8	9		50	46
Stn 8	12	13	17	14	9	10	41	40	40
Stn 11	2	1	6	11	2	0	11	13	12
Main Stn	3	4	8	*	*	*	*	*	*
Stn 17	2	2	9	10	4	4	16	17	17
Stn 19	2	3	8	9	4	5	15	18	17
mean %	22		39		18				

*Temperature extremes were dampened within the Stevenson screen, therefore fewer through-freezing cycles were recorded than were actually experienced at the site.

the rest of the forest-tundra zone is below freezing, is the centres of tree islands. An island monitored in 1970 had only two frost nights for all of July and August, whereas an adjacent patch of tundra had seven and a nearby meadow in an air-drainage channel had 19. In Aug 1970, temperature maxima were significantly lower and minima significantly higher within the tree island compared to an adjacent tundra site (Table 9).

Winter temperatures show a similar correlation with topography. Minima are highest on hilltops and lowest in the valley bottom.

TABLE 9. Unpaired-mean comparison of temperatures at +10 cm within a krummholz clump (K) and an adjacent tundra site (T).

	Maximum K	Maximum T	Minimum K	Minimum T	Mean Difference max	Mean Difference min
June 1970	14.2	16.7	2.9	2.0	2.5	0.9
July 1970	15.4	18.4	4.8	3.6	3.0	1.2
Aug. 1970	16.0	19.4	5.3	3.7	**3.4	*1.6

* = significant at 95% level
** = significant at 99% level

VAPOR PRESSURE DEFICIT

No seasonal pattern of VPD was evident in the Bald Hills (Fig. 7). Mean VPD was generally fairly low. The extreme high was 17 mb on 24 Aug 1969. On Signal Mt., Hrapko (1970) reported 22 mb on the warmest day of the 1967 season. Sustained high values (e.g. No.5, Fig. 3) may be much more closely correlated with success or failure of biological organisms than are mean values.

Vapor pressure deficit is more closely related to water loss in biological organisns than is relative humidity (Williams and Brochu 1969). The daily trend of VPD (Fig. 8) is

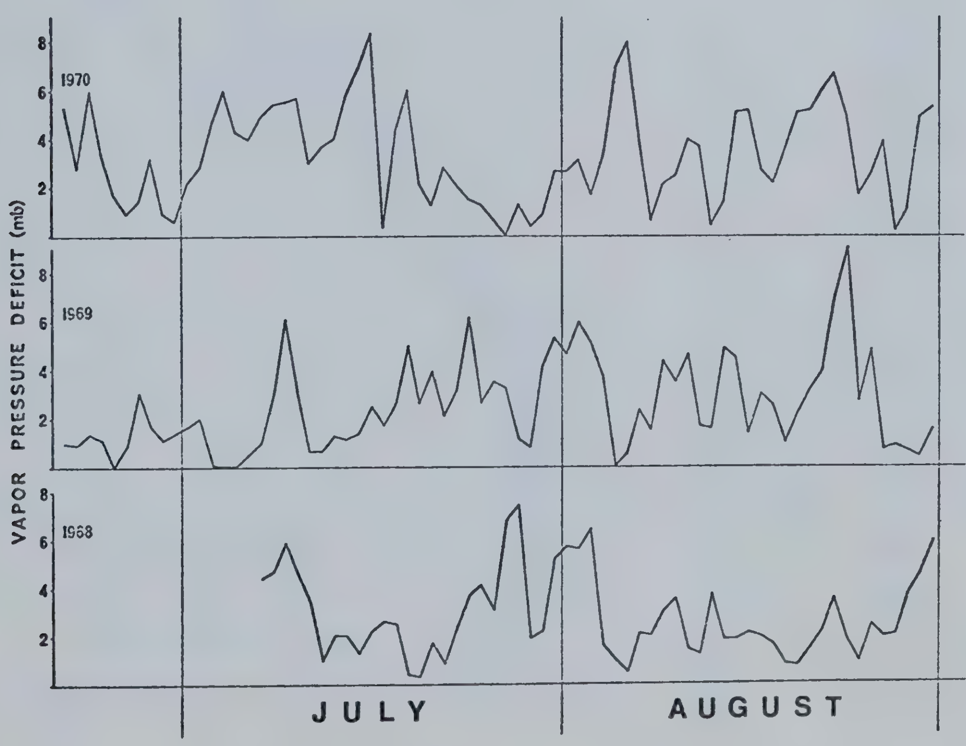

FIG. 7. Mean daily vapor pressure deficits (based on hourly values) at the Main Station, 1968-70.

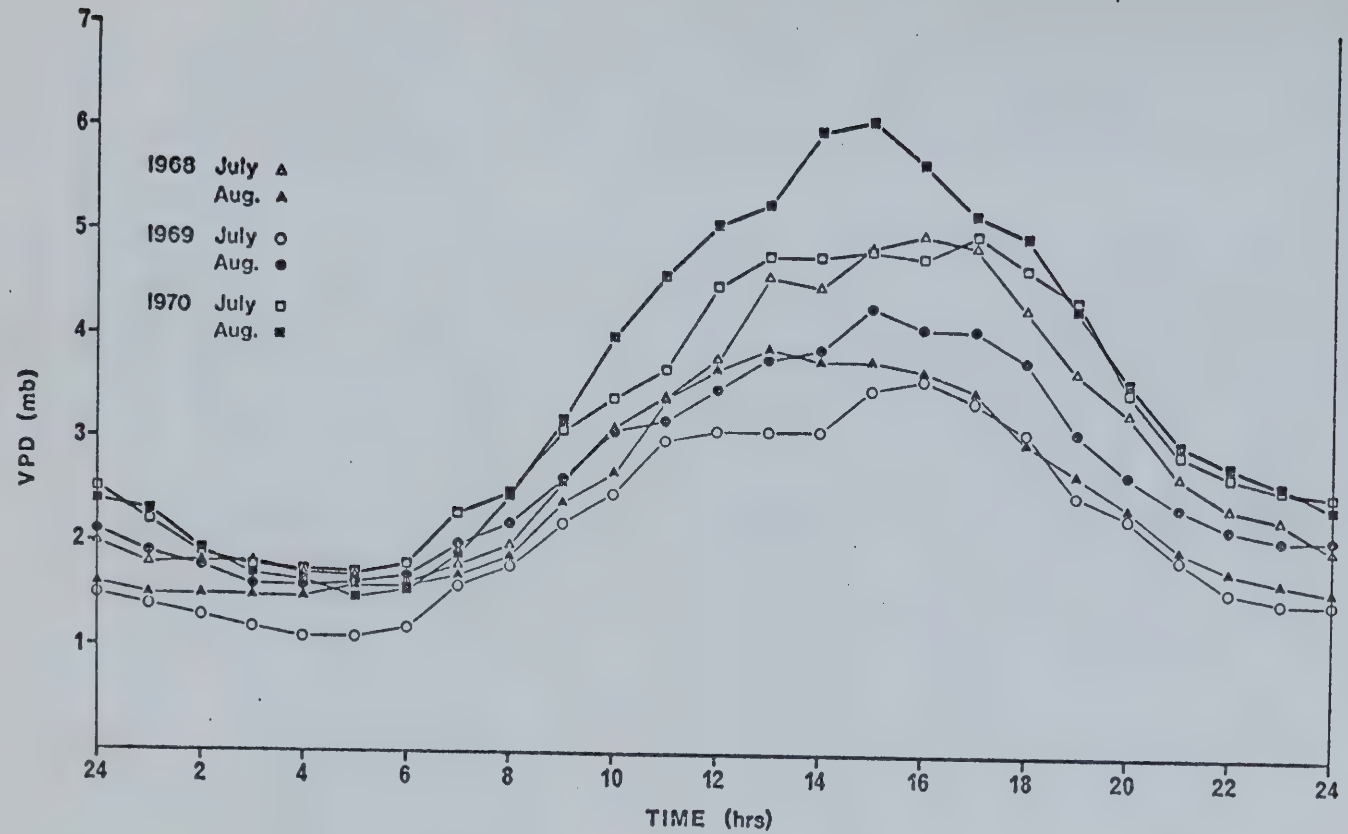

FIG. 8. Daily trend of vapor pressure deficit at the Main Station in July and August 1968-70 (based on hourly means).

a virtual mirror image of relative humidity which in turn is temperature-dependent (Fig. 5).

PRECIPITATION

July plus August precipitation in 1963-70 varied from 77 to 210 mm (Table 2). Rain, occasionally hail or snow, fell in fairly small increments, over 2-4 day periods (Fig. 9). Precipitation was usually well distributed through the season. The entire season could be cool and damp, e.g. 1968, or warm and dry, e.g. 1967 (Fig. 9).

On 6-7 Aug 1969, a 91 cm snowfall was recorded in the Bald Hills. Meltout was complete within a week. Meadow vegetation was flattened, but no serious permanent effects were evinced.

WIND

Mean July-August windspeed (+40 cm) at the Main Station was 1.88 m/sec (Table 7). The values between years and months are rather close. No real trends are apparent between or within years (Fig. 10). Windspeeds above 20 m/sec are very rare. Hrapko (1970) reported a mean of 2.78 m/sec (at +2 m) for the summer of 1967 at Signal Mt.

Winter windspeeds in the Bald Hills are not much higher than summer (Tables 6,10). Recorded windspeeds in most alpine areas are somewhat to much higher in winter than in summer (Judson 1965), and summer windspeeds are generally somewhat

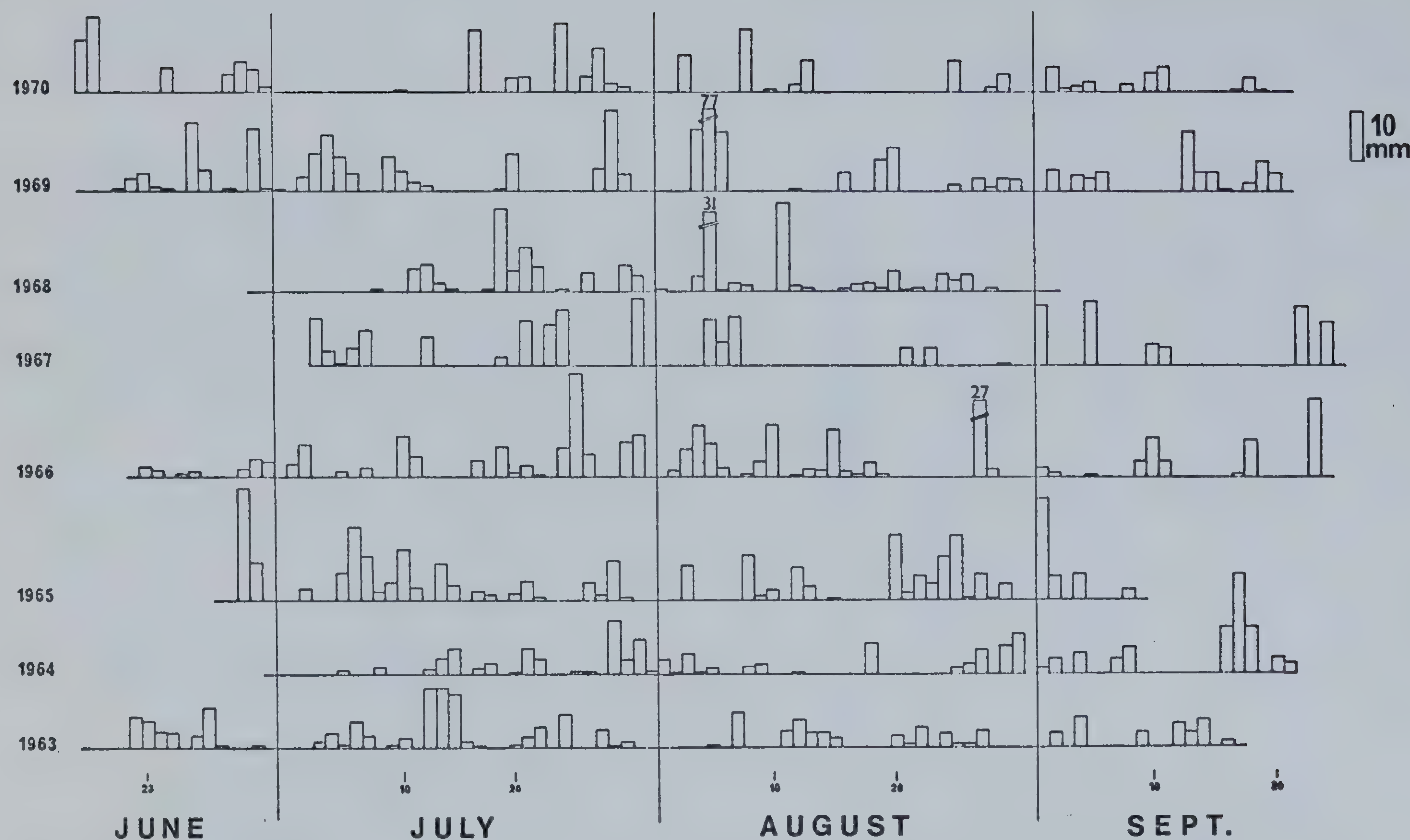

FIG. 9. Summer precipitation at the Bald Hills fire lookout, 1963-70.

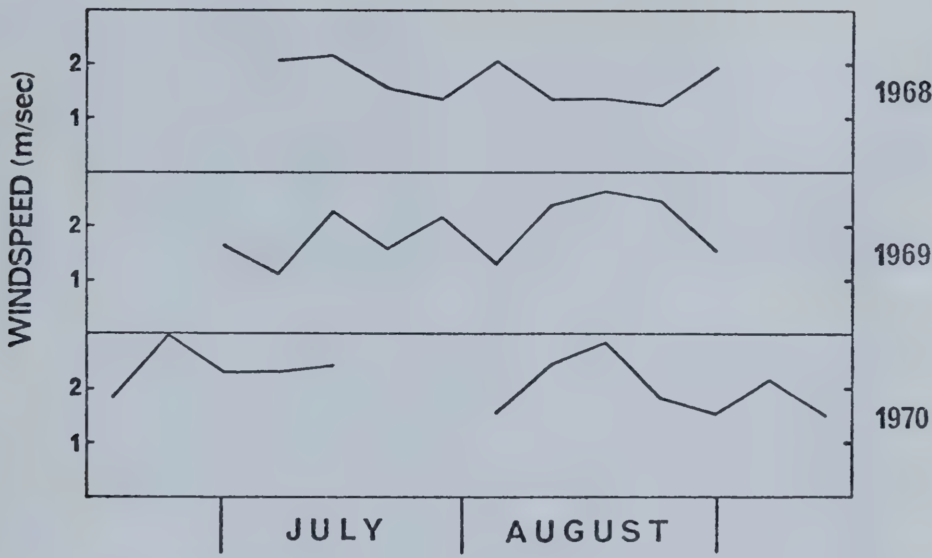

FIG. 10. Mean weekly windspeed (÷40 cm), summer 1968-70, at the Main Station.

TABLE 10. Mean windspeed at 40 cm, on the Bald Hill, 1970-71.

INTERVAL	MEAN WINDSPEED m/sec
21 Sep - 16 Oct	3.76
16 Oct - 11 Nov	2.83
11 Nov - 16 Dec	3.84
16 Dec - 27 Feb	4.23
27 Feb - 26 Apr	3.67
26 Apr - 9 May	3.11
9 May - 28 May	3.64
28 May - 29 Jun	3.11

higher than in the Bald Hills.

Wind is important in its effect on plant transpiration rates. In warm dry weather, the relatively high windspeeds on S and W aspects might increase vapor pressure deficits to intolerable levels for plants, hence their poor development on these slopes.

Wind is also important in snow redistribution. As at Signal Mt. (Hrapko 1970), prevailing winds in the Bald Hills are NW through SW; snow therefore accumulates on the E side of ridges. All of the W slopes are essentially snow-free the entire winter (Plate 5). Some ridge crests and the SW-facing portions of the "balds" (Plate 6) are relatively windy sites (Table 11), snow-free except for very thin (0.5-1 cm), discontinuous crusts of ice and hard snow that form and thaw throughout the winter. In 11 winter trips, I saw these sites essentially bare on all but one occasion, directly after a snowfall and presumably prior to redistribution by wind.

TABLE 11. Comparison of mean windspeed (at 40 cm) at the Main Station (*Phyllodoce glanduliflora-Cassiope* spp.) with that of other sites in the Bald Hills.

COMPARISON INTERVAL	NO. DAYS	LOCATION OF SECOND ANEMOMETER			PERCENT DIFFERENCE
		ELEVATION (m)	ASPECT & DEG. SLOPE	SITE AND COMMUNITY	
4-13 Aug	10	2375	E10	ridgetop *Dryas octopetala*/lichen	74
31 July-17 Aug 69	18	2350	W2	ridgetop *Dryas octopetala*/lichen	57
8-11 July 68	4	2375	S30	*Kobresia bellardii*	45
11-14 July 68	4	2350	W2	ridgetop *D. octopetala*/lichen	44
23-31 July 69	9	2360	SE25	*D. octopetala-Arctostaphylos uva-ursi*	14
19-25 July 68	7	2300	N3	forb meadow	9
26 July-4 Aug 68	10	2320	SE2	mixed, mostly snowbed	-2
18-26 Aug 68	9	2225	SE5	heath & forb tundra	-13
19 Aug-3 Sept 69	16	2200	NE7	*Phyllodoce-Cassiope mertensiana*	-13
14-23 July 69	10	2320	S1	*Phyllodoce-Cassiope mertensiana*	-19
14-19 July 68	6	2350	SE10	heath & snowbed below sharp crest of hill	-30

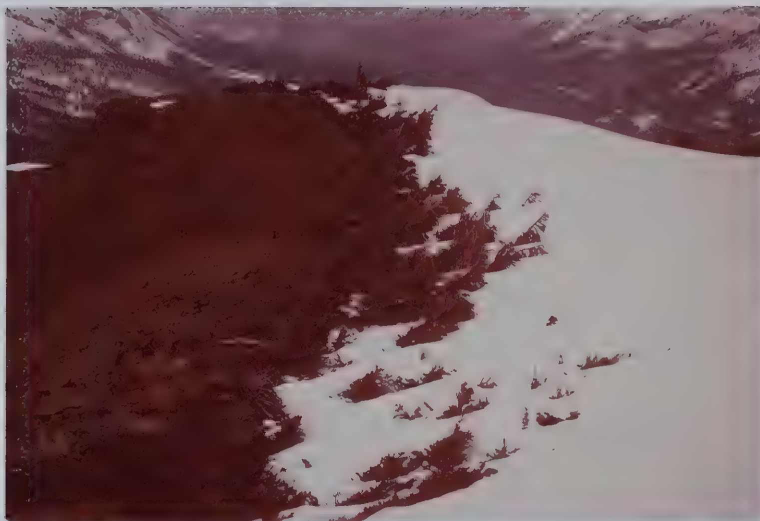

PLATE 5. West ridge of Bald Hills on 26 April 1971: snowfree west-facing slopes, a line of partly covered krummholz along crest, and deeply snow covered heath and snowbed communities leeward.

PLATE 6. Midwinter (24 Jan 1970) appearance of upland tundra: the only snowfree areas are sections of boulder-field subtype of lichen tundra (in foreground), and of *Dryas octopetala*/lichen tundra (centrally and on far hill).

Heath and snowbed communities occupy sites with relatively low windspeeds (Table 11). Correlation of snow pattern with specific plant communities is discussed in Chapter 5.

Density of snow in very windy sites - windslab - was 0.4-0.5. Most other sites had low densities in Nov-Dec (0.1-0.2), rising to 0.5-0.6 by May. Snow density varied much more in a vertical rather than horizontal plane, and did not seem to correlate with the mosaic of plant communities.

SOILS

Soils in the Bald Hills have developed mainly on a thin layer of glacial till, derived from local shales and conglomerates and deposited during Pleistocene glaciation. Shallow lithic contact is found only in areas of rock outcrops and the tops of some of the ridges. Alluvial and colluvial parent materials are unimportant on an areal basis. Alluvium is very local in occurrence in the Bald Hills; and most colluvium is fresh and unstable (i.e. talus), and has negligible plant cover and soil development.

The Bald Hills soils strongly resemble those of other alpine areas in the Canadian Rockies (e.g. Beder 1967, Baptie 1968, Hrapko 1970, Knapik 1973, Knapik et al. 1973). They are extremely young, weakly developed and very coarse-textured due to recent glaciation, slowness of weathering and soil-forming processes, and disruptive action of frost (Beder 1967).

Most soils in the Bald Hills have a high content of pebbles and cobbles (Table 12) and are coarse-textured,

TABLE 12. Physical and chemical properties of some Bald Hills soils.

PLANT COMMUNITY TYPE	ASPECT & DEG. SLOPE	ALT. (m)	SOIL HORIZON	SAMPLE DEPTH (cm)	COARSE FRACTION (% wt)	2mm FRACTION (%)			pH	PPM AVAIL.		
						SAND	SILT	CLAY		N	P	K
Dryas octopetala/lichen	0	2285	L	3-0	24							
			Ah	0-6	28	72	22	6	4.5	4	4	75
			C	6-12	66	54	30	16				
Dryas octopetala/lichen	0[a]	2285	Ah	0-9	63	84	9	7				
			C1	9-20	62	83	9	8				
			C2	20-30	40	74	14	12				
Dryas octopetala/lichen	N2	2300	L	2-0	68				4.9	1	9	90
			L	2-0	53				5.2	1	12	107
			Ah	0-18	33				5.2	0	4	39
Dryas octopetala/lichen		2285	Ah	5-15	18	52	38	10				
			Bm	15-20	48				3.6	4	68	26
			IIC	25-30	8				4.1	3	38	22
			IIIC	40-50	33	80	13	7	5.4	1	2	46
Dryas octopetala/lichen	S2	2330	Ah1	0-5	51	73	14	13	5.0	1	2	51
			Ah2	5-15	61	91	3	6	5.4	0	3	53
			IIC	20-30	30	42	41	17				
			IIIC	40-50	42	51	28	21	5.6	1	12	75
Artemisia norvegica/ *Dryas octopetala*	SE5	2285	Ah	0-10	35				5.0	1	9	65
			Bm	10-28	38	72	19	9	5.2	0	15	58
			IIC	28-38	4	38	54	8	5.9	0	4	47
			IIIC	58-73	49	78	19	5	4.9	1	1	31
Cassiope tetragona/ *Dryas octopetala*	0	2330	Ah	0-4[b]	24				4.1	2	36	31
			Ah	0-4[c]	29				4.0	3	33	43
Cassiope tetragona/ *Dryas octopetala*	0	2330	Ah	0-13	22	74	18	8				
			Bm	15-25	6	64	24	12				
			IIC	25-35	12	65	21	14				
			IIIC	45-55	20	47	36	17				
Cassiope tetragona-*Phyllodoce glanduliflora* subtype			L	2-0	24				4.5	4	27	94
			Ah	0-14	31	58	23	19	4.8	1	3	33
			Bm	18-28	30	72	16	12				
			C	48-53	48	52	30	18				
Phyllodoce glanduliflora -*Cassiope mertensiana*	E3	2330	Ah	0-11	46	75	19	6				
			Bm	11-25	50	72	14	14				
			IIC	25-60	33	65	17	18				
			IIC	60-75	15	50	25	25				
			IIC	75-85	12	64	12	24				
			IIIC	85-95	49	64	12	24	5.1			
Carex nigricans (hummock)	S2	2315	Ah	0-5	8				3.6	7	77	24
			Bm1	8-16	1	30	62	8	5.6	0	3	16
			Bm2	21-26	9	40	52	8	3.8	2	47	57
			C	35-43	51				5.0	1	2	28
Carex nigricans (hummock)	E10	2300	Ah	0-10	1	60	34	6				
			Bm1	15-25	0	34	56	10				
			Bm2	28-32	0	30	65	5				
			C	53-57	0	20	71	9				
Luzula snowbed	NE15	2285	Ah	0-4	79	86	6	8	5.6	1	10	59
			C	4-12	66	84	8	8	5.3	1	8	59
			C	12-30	58	86	6	8	5.5	1	11	61
			C	30-55	53	85	7	8	5.5	0	13	75
bare (snowpatch)	0	2250	C1	0-2	31	74	18	8	4.9	3	14	59
			C2	2-8	18	71	17	12				
Artemisia norvegica-*Anemone occidentalis*	E35	2225	AC	10-30	35	70	24	6				
Artemisia norvegica/ *Salix arctica*	0	2315	Ah	0-8	23				4.8	1	4	53
			Bm	8-25	8	38	34	28	5.4	1	3	39
			C1	25-60	22				5.2	1	4	37
			C2	60-75	38	44	26	30				

[a]Slight depression.

[b]Under *Cassiope tetragona*.

[c]Under *Dryas octopetala*.

mainly sandy loams with some silt loams, loams and clay loams. They are acid to highly acid (pH 5.9-3.6), and pH increases with depth. Frost action has disrupted many of the profiles. The commonest effects are (1) burial of A horizons in solifluction terracette fields, and (2) formation of silt bands and lenses in hummocky tundra. Knapik et al. (1973) reported thin layers and lenses of volcanic ash in tundra soils from Banff Park, and ash deposits to 1 m thick in small depressional areas. The latter has not been observed in the Bald Hills. On Signal Mt., Hrapko (1970) recorded soil pH values between 6.5 and 4.5; generally low nitrate and phosphate values; and very variable potassium. A similar pattern obtains in the Bald Hills (Table 12), though pH values seem slightly lower.

Much of the upland tundra in the Bald Hills has a very simple soil profile of rocks, pebbles and fines that show little change with depth. Classified as Orthic Regosol, this soil type is characterized by a thin, discontinuous A horizon over rocky, relatively unaltered material, and lacking a B horizon. The parent material is loose and near the surface. Even less altered are Orthic Regosols in extremely late-melting snowbeds with little or no plant cover. There is typically a homogeneous profile of small loose pebbles exhibiting very little chemical or physical change with depth (cf. *Luzula* snowbed, Table 12).

An Orthic Regosol profile is described below. It is site S38, altitude 2330 m, on a 2^{o} S-facing slope. The

rapidly drained pedon supports a *Dryas octopetala*/lichen community.

Horizon	Depth (cm)	Description
L	2-0	Discontinuous *Dryas* turf; abundant, conspicuous fine and medium roots; clear boundary; 0 to 3 cm thick.
Ah	0-15	Yellowish gray (2.5Y 5/3) gravelly loamy sand; weak, fine granular; very friable; fairly abundant, conspicuous roots; 55% coarse fragments; strongly acid; irregular boundary.
IIC	15-40	Yellowish gray (2.5Y 5/4) clay loam; weak granular?; some roots to 30 cm, very few beyond; 30% coarse fragments; medium acid; abrupt, irregular boundary.
C	40+	Dull yellow (2.5Y 5.5/3) gravelly clay loam; loose; exceedingly few, fine roots; 40% coarse fragments; medium acid.

Under high or complete plant cover in mesic sites there is better soil development. B horizons are present, and the soils are classified as Brunisols. Most soil profiles in heath-dominated tundra are Alpine Dystric Brunisols. A fairly typical profile is described below. It is site S11, altitude 2330 m, on a 3^{o} E-facing slope. The well drained pedon supports a *Phyllodoce glanduliflora-Cassiope mertensiana*

community.

Horizon	Depth (cm)	Description
L	5-0	Brownish gray (10YR 4/1.5) turf; abundant, fine and medium roots; strongly acid; clear, wavy boundary; 4 to 8 cm thick.
Ah	0-6	Dark grayish yellow (2.5Y 4/2), grayish yellow brown (10YR 4/2) clay loam; weak, finely granular; friable; fairly abundant, fine roots; strongly acid; clear, wavy boundary.
Bm	6-16	Dull yellowish brown (10YR 5/4), dull yellowish orange (10YR 6/3) clay loam; weak, medium platy; few, fine roots; 10% coarse fragments; strongly acid; irregular boundary; 8 to 18 cm thick.
IIBm	16-26	Dull yellowish brown (10YR 5/4) silt loam; medium subangular blocky; few, fine roots; only 1% coarse fragments; strongly acid; clear, wavy boundary.
IIC	26-55	Dull yellow (2.5Y 5.5/4) gravelly sandy loam; medium subangular blocky; very few, fine roots to 40 cm; 60% cobbles; strongly acid; irregular boundary.
C	55+	Yellowish gray (2.5Y 5/4) sandy loam.

Correlation between soil subgroups and vegetation types in the Bald Hills is not very good. In general, Orthic Regosols support rocky upland tundra communities, while Alpine Dystric Brunisols support heath-dominated vegetation. There are exceptions, as Knapik (1973) has shown in an alpine tundra area of Banff Park. For example, communities dominated by *Cassiope tetragona* may have Orthic Regosols, Cumulic Regosols, or Alpine Dystric Brunisols (Knapik et al. 1973).

There is better correlation between soils and some of the less important plant community types in the Bald Hills. Cumulic Regosol profiles on steep slopes where the soil pedons have been churned up by gravitational movement support herb meadow vegetation, specifically the *Artemisia norvegica-Anemone occidentalis* community type (cf. p.108). Cumulic Regosols on gently sloping, recent alluvial deposits have willow scrub or certain herb meadow communities. Bog communities have poorly drained Gleysolic soils.

5. VEGETATION

METHODS

Reconnaissance

The first field season, 1968, was spent in environmental monitoring and general familiarization with the flora of the study area. Tentative community types were delineated, and phenology pursued to some extent.

In 1968-71 I visited tundra areas in Jasper Park and other Cordilleran regions, to get some idea of geographical relationships of the Bald Hills plant communities and the regional status of *Dryas*. My 1972-73 involvement in vegetation studies at Waterton Lakes National Park (Kuchar 1973) and Yoho National Park (Kuchar unpubl.) enabled me to supplement Bald Hills data, especially in the typification of vegetation dominated by *Dryas octopetala*.

Stands

Most of the quantitative data on plant community structure and composition were gathered in 1969. I subjectively chose representative stands (Fig. 2) of areally important community types, and of some uncommon but unique or atypical types. Criteria for stand selection were: 1) 11x21 m minimum size; 2) by visual inspection no clinal variations of plant cover, plant composition, or physical habitat; 3) within the stand, no pockets larger than 1 m^2 of vegetation belonging to a different community type. Sampling dates were in most instances sufficiently late for full expression of vascular

plant phenology and cover.

Thirty 25x25 cm quadrats were used in 18 of the 21 stands. Twenty-five 20x50 cm quadrats were used for more precise quantification of plant cover in one stand, site of intensive invertebrate studies. One hundred quadrats were used in each of two low-cover stands. The 25x25 cm quadrat was used in another alpine study in the park (Hrapko 1970), and is a more appropriate size for estimating coverage of small clones of lichen and bryophytes than the more commonly used 20x50 cm quadrat. Isodiametric quadrats are theoretically inferior to rectangular ones (Daubenmire 1968), but not by much since there is the perimeter factor. The 20x50 cm size seems to be traditional in North American studies of alpine vegetation. Its use can be traced to Cain (1943), who advocated it as the ideal size. However, his conclusions were based on what can hardly be called exhaustive study, in variety of tundra types as well as sampling schemes. Eddleman et al. (1964) investigated different sizes, numbers, and shapes of quadrats and concluded that shape was not important. They stressed quadrat size, and indicated that for tundra vegetation, 4 dm^2 quadrats were as suitable as 8 or 16 dm^2 ones.

A random numbers table was used to establish coordinates for quadrat placement in each 10x20 m plot. Within each quadrat, visual cover estimates were made using this scale: +<1%, 1=1-5%, 2=6-15%, 3=16-25%, 4=26-50%, 5=51-75%, 6=76-95%, 7=ca.100%. Estimates included: each distinguishable taxon of vascular plants, bryophytes and lichens; ground surface type;

total cover of vasculars, of bryophytes, and of lichens. True cover, i.e. the vertical projection on the ground of living plant parts, was used rather than "canopy cover" (Daubenmire 1968). The major drawback of true cover was its de-emphasis of mat-forming species especially *Dryas octopetala*, whose low live shoot cover belied its ecological weight.

As a standard with which to compare the degree of accuracy of cover estimation I also used the point-sample method in the first stand. In each quadrat I took two rows, perpendicular to one another, of 25 point samples each. At 1 cm intervals on a wooden sampling frame, no. 12 knitting needles with sharpened points were lowered vertically and all hits recorded. My subjective estimates were high, so I adjusted quadrat cover values. I compared visual and point-sample estimates again in the ninth stand.

Cover was selected as the most important parameter of a plant's abundance and biotic influence. Unfortunately, only in exceptional communities was the vegetation homogeneous enough to permit a good cover estimate of most species when thirty quadrats were used. I had intended to use rigorous 95% confidence limits, viz. 10% of mean cover of the more important species; however, literally hundreds of quadrats would have been required in almost all stands. My choice of 30 quadrats was a compromise - it gave the floristic picture and good estimates of total cover of major plant groups (Table 13), but poor estimates for most species. Thirty 25x25 cm quadrats, or 1.88 m^2, compare favorably with the commonly

TABLE 13. Ninety-five percent confidence interval expressed as a fraction of cover estimates of major plant groups in six stands.

VEGETATION TYPE	STAND NO.	VASCULAR PLANTS	BRYOPHYTES	LICHENS	TOTAL VEGETATION
Heath tundra	9	0.12	0.19	0.16	0.09
	14	0.09	0.19	0.21	0.07
	15	0.12	0.28	0.22	0.08
Dryas/lichen tundra	6	0.43	0.43	0.21	0.18
	7	0.30	0.51	0.15	0.11
Forb meadow	21	0.12	0.14	0.57	0.08

used twenty 20x50 cm quadrats, or 2.00 m^2. In stands 29 and 30 (Table 16, p.81), the very low % plant cover (and therefore higher sampling speed) prompted me to use a larger number of quadrats. Very low standard errors of the means, and the low numbers of species not found in the quadrats, are suggestive of adequate sampling intensity.

Other observations in the stands included: soil temperatures at -15 cm, taken four times in the 1970 season; plant stratification and heights; slope and aspect; flowering and fruiting of vasculars; plant species absent from the quadrats; topography; cryopedic features; wind deflation features; miscellaneous (e.g. burrows).

Transects

Three transect studies were done (Fig. 2): (1) on *Dryas*-dominated tundra on top of the Bald Hill; (2) across a snowbed-meadow complex; (3) in a coenocline from *Dryas*/lichen through to *Carex nigricans* community.

(1) Three baselines, 375, 55 and 35 m long, were established over *Dryas*-dominated tundra on the Bald Hill. At 5 m intervals, two 25x25 cm quadrats were set out at random distances of 1-10 m perpendicular to the line. Estimates were made of each vascular plant species' cover; total cover of each of vascular plants, bryophytes, and lichens; cover by major ground surface types.

(2) A baseline was established across herb-dominated vegetation in a slight depression trending up a very gentle SE-facing slope. Eleven 20x50 cm quadrats were laid down at 2 m intervals. Then came three series of 3 quadrats at 2 m intervals, each series separated by 10 m. All quadrats were oriented with long axis perpendicular to slope. Percent cover of all vascular plants and cryptogams was estimated in each quadrat.

(3) A N-S baseline was established over the rounded top of a small hill and down the 5-10° N slope, cutting across six distinct plant communities. Ninety-one 20x50 cm quadrats were laid down at 0.5 m intervals, long axis of each perpendicular to slope. Cover estimates included: all recognizably different vascular and non-vascular plant species; total cover of each of vascular plants, bryophytes and lichens; ground surface type. Soil temperature (-15 cm) and % soil moisture (at 0-8 cm) were determined three times in the season. Phenological notes were taken at approximately two-week intervals in 1969.

Other vegetational studies

Some plant communities, notably small, poorly developed or floristically simple ones, were not sampled quantitatively. Species lists were made, dominants noted, general habitat descriptions secured, and some phenological events followed.

The small hill just south of the lookout was chosen as a good site of forest-tundra vegetation. A 45x135 m tract was inventoried for numbers and kinds of conifer groupings and associated ground vegetation.

Micro-community patterns were studied, but these are related in Chapter 7.

Phenological notes were taken throughout the 1968-70 seasons, and during trips in 1971 and 1972. I usually noted flowering, fruit development, and fruit dispersal. Phenological curves and profiles were drawn up, based on presence of flowers, fruit, and shedding fruit.

Synthesis

Mean, standard deviation, standard error of the mean, and percent quadrat frequency were calculated for cover estimates in each of the sampled stands. The second and third transects were sectioned into what appeared to be natural communities, and the above calculations made within each. The 199 commonest plant species of the stands were selected. No species was omitted that had a quadrat frequency greater than 15% or mean cover greater than 0.5% in any stand. Prominence Values (PV = mean cover x frequency^{-2}) (Stringer and La Roi 1970) were calculated for each species in each stand.

Similarity coefficients ($C = 2w/(a+b) \times 100$) were computed between all possible stand pairs. The stands were ordinated using Easton and Precht's (ca. 1973) ordination program based on Beals (1960) and Bray and Curtis (1957). Ordinations were based on Prominence Values as well as mean cover values. Whittaker and Gauch (1973) recommend the Bray and Curtis method over other types of ordination, for its clarity of technique and relative freedom from distortion.

CLASSIFICATION

Vegetation units

By avoiding overt gradients while selecting stands, I was optimizing the chances of finding (and describing) near-peak or nodal expressions of different plant assemblages, viz. community types. These are abstract units of low rank that represent the theoretical "noda" of the study area's vegetation. I considered dominant species in major strata as the most important criterion in the delineation of community types. Most types were named after the two species with highest percent cover. Distinct and usually recurring structural or compositional variants were assigned subtype status.

Community types were organized into Groups, based chiefly on growth form in the dominant layer(s) and on site conditions especially soil moisture. These Groups correspond to alliances of European phytosociology, and the community types correspond to, or perhaps are used in a slightly broader sense than, associations. Whittaker (1973) recommends the

criteria used above in vegetation classification. He considers the first split, based on structure, as traditional; and the second split, the use of dominant species, to be a self-evident and natural choice.

Classification of Bald Hills vegetation

Bald Hills tundra embraces four major Groups of plant communities: Stony Tundra, Heath Tundra, Herb Meadows, and Snowbeds (Table 14). Stony Tundra occupies exposed, sometimes rather unstable sites: hilltops and ridge crests, S and W-facing slopes, some steep E-facing slopes. Most communities of the Group have a coarse surface of various-sized pebbles, sometimes boulders; virtually no soil development (Regosol); a windy, xeric environment; rock lichens; *Dryas octopetala* and/or cushion and rosette vasculars. Frost-patterned ground features are common. There are two Subgroups, one characterized by the dominance of *Dryas octopetala* and the other by its total or virtual absence.

Heath Tundra is developed on mesic N and E-facing slopes and locally on W-facing slopes. It is most prominent within and immediately above the forest-tundra zone (Appendix 4). The Group is a tight-knit one: most communities have a high and homogeneous[1] cover of mountain heathers in the genera *Cassiope* and *Phyllodoce*; there is, for alpine vegetation, relatively good soil development (often Orthic Brunisol); the

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[1]Cf. Table 14: the ratio of mean cover to standard deviation, an estimate of dispersion, is relatively high.

TABLE 14. Mean and standard deviation of cover estimates in some vegetation stands and transect segments.

MAJOR VEGETATION GROUP	COMMUNITY TYPE	QUADRAT SIZE (dm^2) & NO.	STAND NO.	VASC.	BRYO.	LICH.	ROCKS	PEBBLES	SOIL	LITTER	MEAN NO. SPP./QUADRAT			TOTAL NO. SPP.		
											VASC.	BRYO.	LICH.	V	B	L
DRYAS TUNDRA	*Artemisia norvegica/ Dryas octopetala*	6/30	1	10+9	2±4	17±15	0	21±21	1±2	32±21	9±2	3±1	7±2	22	7	18
	Dryas octopetala/ Polytrichum piliferum	6/30	2	14±11	20±17	29±17	x	5±10	14±20	23±14	6±3	5±1	9±2	25	15	28
	Dryas octopetala/lichen	10/25	3	10±5	3±3	16±7	7±9	29±23	1±2	36±22	4±2	5±2	22±3	28	14	50
		10/24	4	5±6	2±1	9±10	x	65±41	x	9±15	2±1	2±2	8±4	8	14	31
		6/30	5	-----	-----	-----	7±10	35±29	2±4	22±15	4±2	3±2	11±3	20	11	27
		6/30	6	4±5	3±3	26±15	8±5	55±20	2±1	4±9	1±1	2±2	13±3	10	13	40
		6/30	7	10±9	1±1	34±14	25±16	25±11	5±5	15±11	4±2	2±1	15±2	21	8	37
HEATH TUNDRA	*Cassiope tetragona/Dryas octopetala*	0/ 9	8	25±18	6±4	17±6	0	5±7	12±20	32±12	7±2	5±1	9±1	16	16	19
		6/30	9	32±13	12±7	23±10	x	5±5	2±4	28±10	7±1	6±2	9±2	18	12	19
		6/30	10	-----	-----	-----	x	-----	-----	-----	9±2	4±1	7±1	25	11	21
		6/30	11	-----	-----	-----	1±	7±10	11±8	29±13	9±2	4±1	8±1	20	9	18
		6/30	12	-----	-----	-----	7±	x	6±6	28±10	8±2	5±2	9±2	22	15	23
		6/30	26	14±10	9±8	40±19	x	24±20	3±6	17±15	7±2	4±1	9±2	21	12	21
	Phyllodoce glanduliflora -Cassiope mertensiana	10/ 8	13	35±6	8±6	13±5	0	0	3±4	48±17	9±1	6±1	6±1	16	12	14
		6/30	14	39±11	19±10	13±8	1±x	x	2±3	30±12	7±2	4±1	5±1	21	15	15
		6/30	15	42±13	12±10	15±9	x	x	1±3	47±17	6±2	5±2	5±1	16	10	15
		6/30	16	38±12	16±7	12±14	2±3	+	1±2	45±15	6±1	5±1	3±1	11	15	14
		10/16	18	39±6	18±11	7±6	0	0	x	39±14	6±1	6±2	5±1	13	18	11
	Luetkea pectinata	10/ 9	17	36±6	38±11	9±8	0	0	0	30±9	10±1	5±2	5±3	18	14	13
		10/15	19	44±15	22±9	4±3	0	0	x	36±10	6±2	4±2	4±1	13	14	11
HERB MEADOW	*Artemisia norvegica/ Salix arctica*	10/ 9	20	32±9	23±9	17±10	0	0	0	34±7	11±2	4±1	7±1	20	5	14
		6/30	21	46±16	47±18	1±1	0	0	x	30±13	13±3	6±2	1±1	40	23	8
	Artemisia norvegica - Luzula parviflora	6/30	22	53±17	40±17	6±8	0	0	x	22±11	11±2	6±2	2±2	31	17	12
	Artemisia norvegica Anemone occidentalis	6/30	23	48±17	22±11	4±5	3±9	x	0	32±11	11±2	5±2	2±1	33	12	21
	Artemisia norvegica - Antennaria lanata	6/30	24	27±13	3±3	9±9	0	27±30	1±1	27±13	7±2	3±1	3±1	22	13	16
		6/30	25	35±8	6±5	7±7	0	27±23	x	28±14	9±2	3±2	4±2	29	11	15
SNOWBED	*Carex nigricans*	6/30	27	61±17	10±12	x	x	0	0	37±14	4±2	3±2	x	22	10	4
		10/ 6	28	74±12	2±1	0	0	0	0	27±12	2±1	2±1	0	5	6	0

NOTE: x<0.5

soil is cold, well-drained, rarely low in soil moisture. The only periglacial features are hummocks (in most communities) and small bare patches generated by needle-ice formation and wind. Larger tracts of Heath Tundra often entail a mosaic of two community types, one dominated by *C. tetragona* and *Dryas octopetala* on slight rises and ridges, the other by *P. glanduliflora* and *C. mertensiana* in the depressed sections.

Herb Meadows[1] are found below 2300 m on gentle to steep slopes of E and N aspects. Features possessed by most communities of the Group are: small size (<0.3 ha); discharge of water (and probably nutrients) through the community from melting snowbanks; soils therefore silty or clayey; absence or relative unimportance of periglacial features; high productivity and thick cover of forbs; lichens very low in cover; *Artemisia norvegica*, the binding species of the Group, usually abundant.

Snowbed communities are typically small, lying in concavities, lee sides of ridges and other sites with deep snow accumulation and late meltout. The growing season is shorter than two months, in some years only one month. Graminoids, from sparse to very dense cover, usually far outweigh all

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[1]A variety of appellations is available for Herb Meadow: timberline meadow (Habeck 1969, Baig 1972), alpine meadow (Moss 1955, Beder 1967, Habeck 1967), subalpine meadow (Kuramoto and Bliss 1970, Douglas 1972), forest/tundra meadow (Kuchar 1972), chionophilic meadow (Kuchar 1973).

other plant groups.

Due to their local nature, small size and unique structure, flora or habitat, six community types do not fit into the above scheme. These include conifer-dominated areas, willow and other scrub, and boggy or marshy sites.

Ordination

Ordination using Prominence Values proved virtually identical to that based on cover values alone (cf. also Achuff 1974), so I selected the latter. A simple correlation coefficient was computed between interstand distance and corresponding matrix dissimilarity values for all pairs of stands. A highly significant correlation ($r = +0.75$, $P<0.01$) suggested that the ordination depicted the similarity matrix in a reasonably faithful manner.

Ordination was not used to identify or even suggest the community types or major "noda", but rather as a relatively objective validation of the classification. Since the low sampling intensity missed some community types, I would have been hard pressed, using what data I had, to derive a definite classification of the Bald Hills vegetation through synthetic, inductive or other statistically-based techniques. Lambert and Dale (1964) contend that it is probably better to start classifying immediately, and ordinate later.

In my opinion, the delineation of major and minor community types can be helped as much by experience as by the gathering and synthesis of quantitative data. Some communities can be readily spotted in the field, and little experience is needed to characterize them. Others are more subtle, and

only some or a good deal of familiarity with the area's vegetation may be a prerequisite for their detection. Here is where experience has been stressed by European phytosociologists.

Distribution of stands on the ordination

The ordination using all stands and transect segments is displayed in Fig. 11. Most of the stands are clustered in the lower left portion of the field. The two snowbed (nos. 27,28) and cushion-rosette (nos. 29,30) stands are isolated

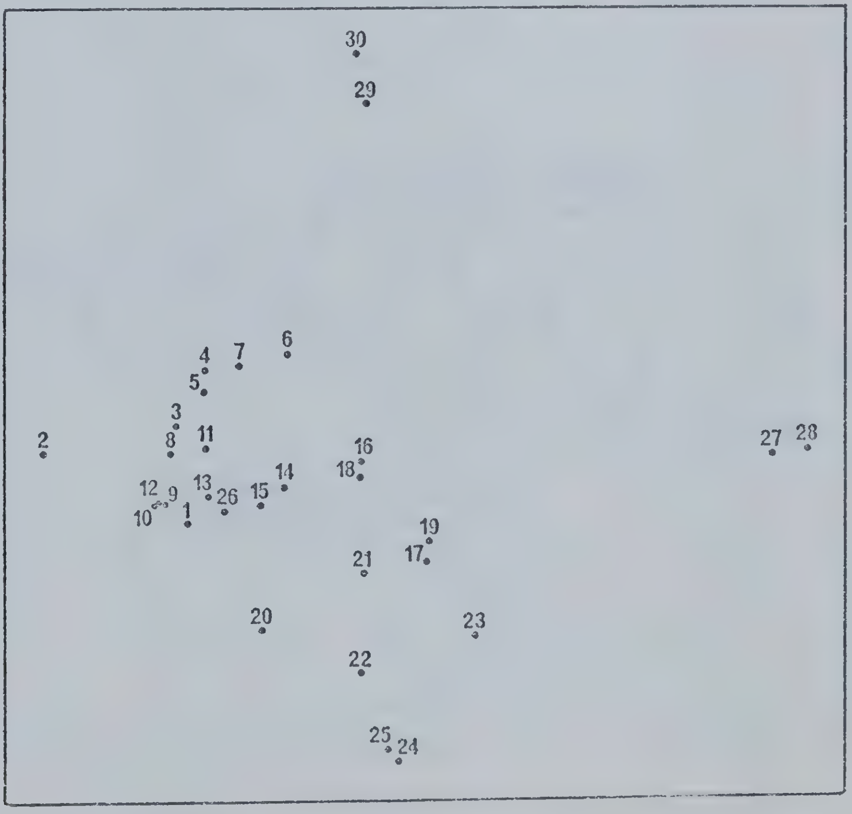


FIG. 11. Distribution of all stands on the o: nation field.

from the others. Though this comes as no surprise, considering their extreme dissimilarity (Appendix 5), the clustering effect tends to obscure stand interrelationships. To increase the spread I excluded stands 27-30 and re-ordinated the data. The new ordination (Fig. 12) proved much more satisfactory and was used thereafter.

There is strong separation along both axes (Fig. 12), and mild clustering in the upper middle of the field. The stand distribution may be explained as a curving coenocline.

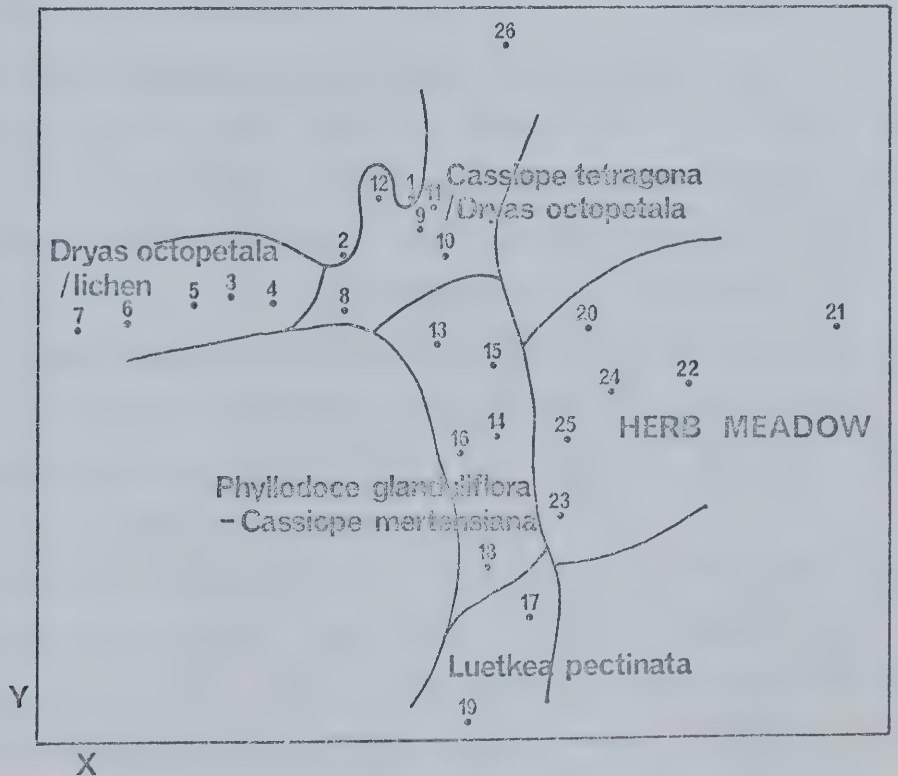


FIG. 12. Distribution of stands on the ordination field (stands 27-30 excluded from the ordination), and the major noda of Bald Hills vegetation that they represent.

Ordinations when viewed in a two-dimensional form often produce distorted coenoclines, sometimes (as here) in the form of an arch (Whittaker and Gauch 1973).

Major noda on the coenocline include *Dryas octopetala*/ lichen communities at the very left, *Cassiope tetragona*/*D. octopetala* at upper left-centre, grading into *Phyllodoce glanduliflora*-*Cassiope mertensiana* and, at the bottom, *Luetkea pectinata*. Herb meadows are positioned near the mesic portion of the heath sequence, but form a group apart from the coenocline (as one might expect, since they are probably not a zonal tundra type).

Distribution of community attributes on the ordination

Environmental variables and vegetational attributes were plotted on the ordination field, and isocenes (Whittaker 1972) drawn (Figs. 13,14). This was not done for altitude, aspect, slope, or litter cover, since little or no correlation was evident between these and plant species or community patterns. There may be a correlation with mean daily surface or near-surface temperature in July and August, but too few sites were monitored to present an adequate trend.

A trend is seen along the coenocline between major community types and percent rock cover, snowdepth, and snow release dates (Fig. 13). From *Dryas*-dominated vegetation through the heath sequence to *Luetkea pectinata*, there is progressively greater winter snowcover, later snowmelt dates, and decreasing rock cover. Both herb and shrub cover rise along the coenocline. Total plant cover increases, but lichen cover decreases

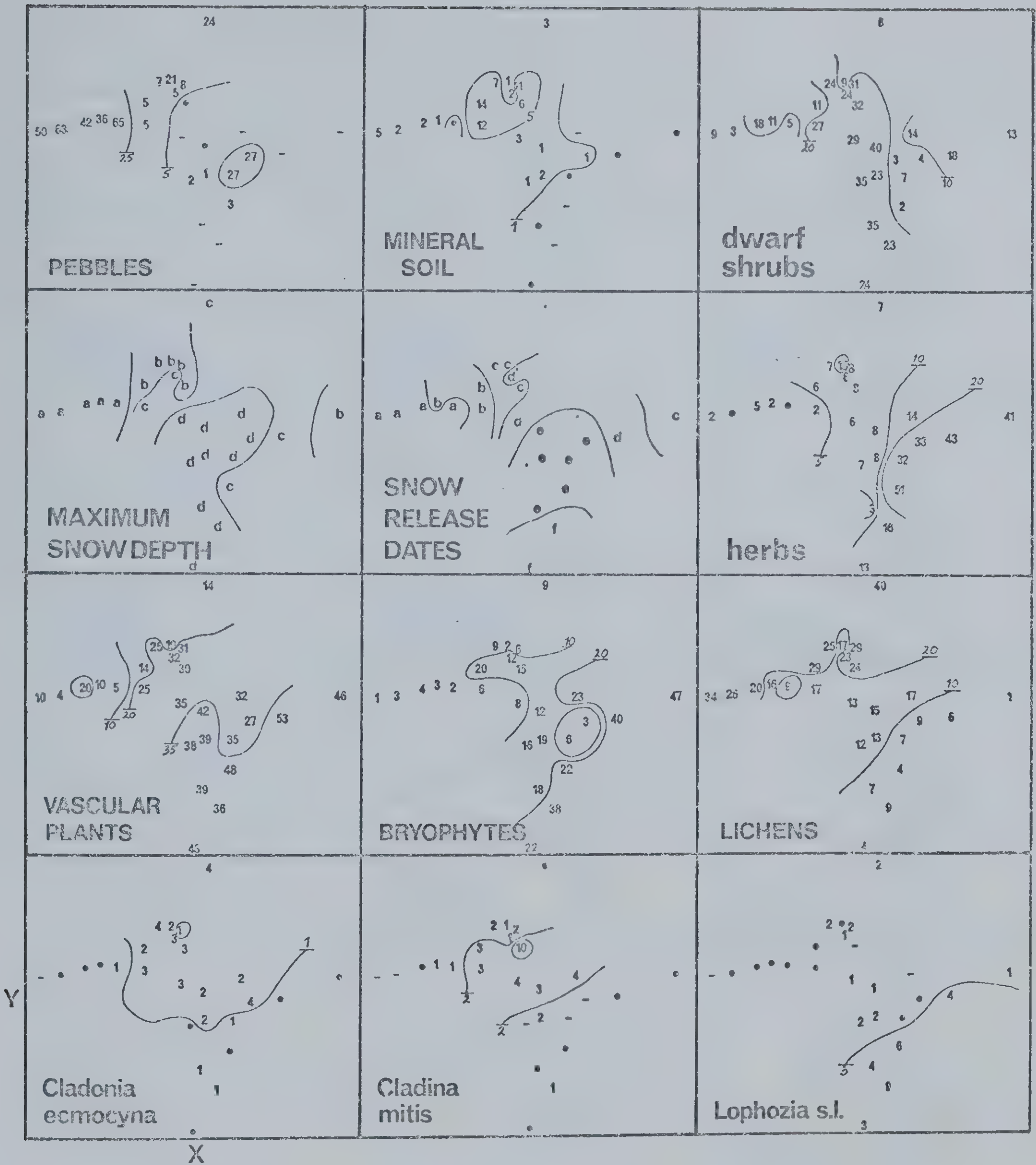


FIG. 13. Some environmental variables and vegetational attributes on the ordination field. All are expressed as % cover (with • <0.5%), except: maximum snowdepth (a<5 dm, b=5-10 dm, c=10-20 dm, d>20 dm), snow release dates (a=before 10 May, b=10-20 May, c=21-31 May, d=1-10 June, e=11-20 June, f=later than 20 June).

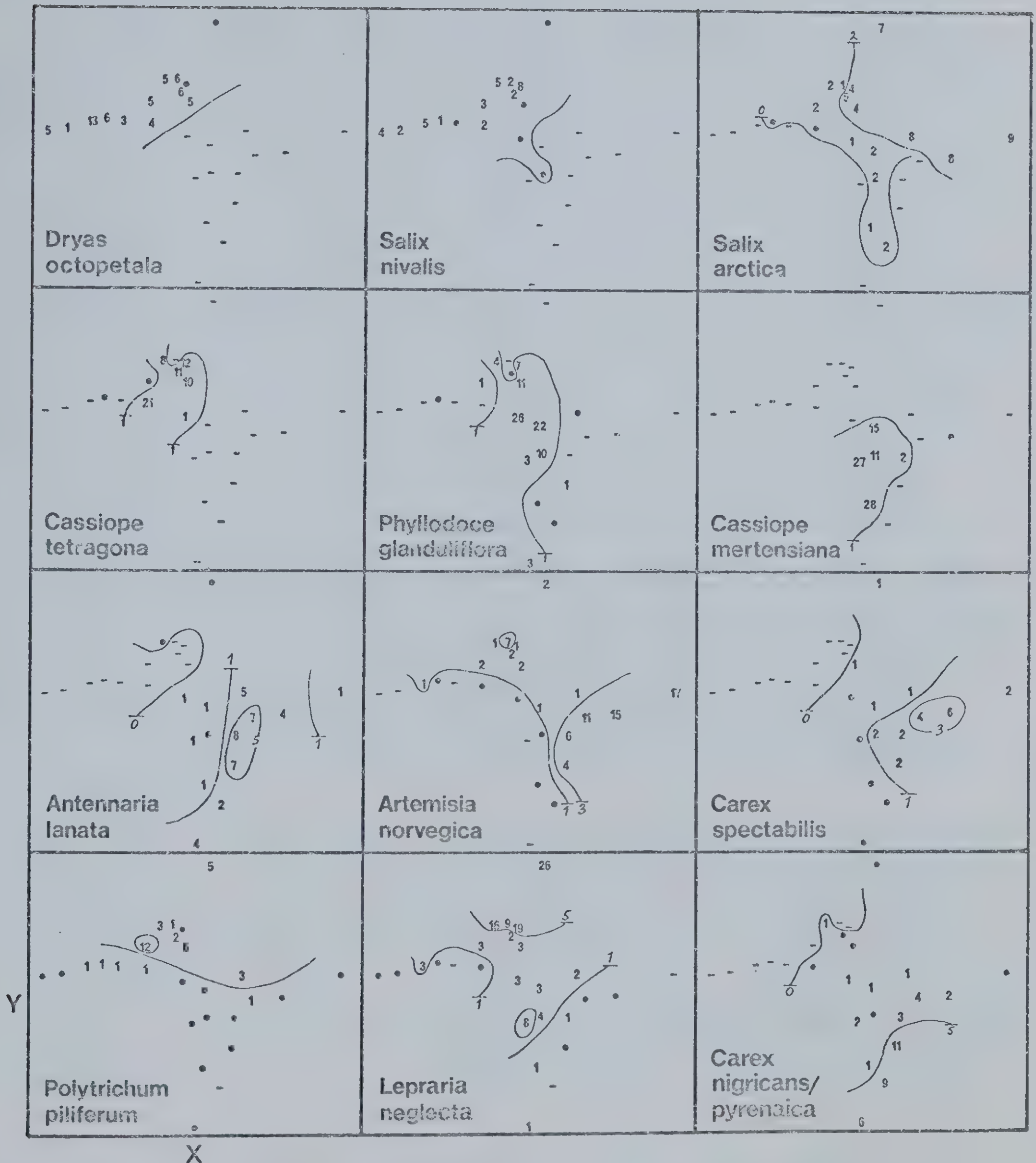


FIG. 14. Percent cover of some plant species on the ordination field. • <0.5%.

Watch trim at front
folded shts

MDK

<u>DRYAS</u> <u>OCTOPETALA</u> AND TUNDRA - BALD HILLS, JNP KUCHAR Ph.D. 1975

2 copies
Black 096

as open, lithic sites are transmogrified into a vegetational canopy. Highest vascular plant cover and lowest lichen cover are in the herb-dominated group.

Most plant species, including those with high cover (Fig. 14), show clear-cut polarization. *Dryas octopetala* and *Salix nivalis* (and also all saxicolous lichens) are strong in the left section of the ordination field that reflects early snowmelt and relatively xeric conditions, but are wanting elsewhere. The heaths (*Cassiope* spp., *Phyllodoce glanduliflora*) are strong in the mesic central portion but very rare or absent elsewhere. *Artemisia norvegica, Carex spectabilis*, and many other herbs are best represented in the right part of the field, signifying continuous moisture supply from melting snowbanks. *Lophozia* s.l. and *Carex nigricans/pyrenaica* (and *Luetkea pectinata*, found only in stands 16-19) are correlated with very late-melting snowbeds. *Antennaria lanata* (and *Sibbaldia procumbens*) is situated medially between snowbeds and herb meadows.

Cassiope tetragona, Phyllodoce glanduliflora, Lepraria neglecta and *Polytrichum piliferum* peak in the upper centre, in what might be termed the meso-xeric nodum. Notable is the correlation of the two cryptogams with peaking mineral surface cover - their ability to colonize denuded surfaces is reflected in their high cover here.

There are no species equally abundant throughout the ordination field. Nearest this condition are some lichens of wide ecological amplitude (also cf. Appendix 6), e.g. *Cladonia*

ecmocyna and *Cladina mitis* (also *Stereocaulon alpinum, Cetraria ericetorum/islandica, Cladonia coccifera/pyxidata*); but even these exhibit definite habitat preferences.

In conclusion, the stand distribution on the ordination field may be explained in terms of snow depth, snowmelt, and available soil moisture through the season together with second-order factors such as slope, aspect, soil temperature. *Dryas*-dominated communities are associated with gravelly, thinly snow-covered and early-melting sites. Heath communities dominated by dwarf shrubs, form an ecological series with three noda, relatively xeric sites with *Cassiope tetragona*, mesic *Phyllodoce glanduliflora-Cassiope mertensiana*, and meso-hydric *Luetkea pectinata* where snowdepth is greatest and meltout latest. Heavily vegetated herb meadows stand apart from the *Dryas*-heaths coenocline. They are probably correlated with even moisture supply rather than with snowdepth or meltout times.

PLANT COMMUNITY TYPES

Stony Tundra Group

1. *Dryas octopetala*/lichen type (stands 3-7, Table 15).

This community type covers the most area of any in the Bald Hills, in a wide elevational range. It is represented on stable ridge crests and gentle slopes of all aspects, and is exposed to wind from most directions. The ground surface is a mixture of pebbles and sand (Plate 7), or may have a

TABLE 15. Percent cover and frequency (in italics) of plant species in stands of the *Dryas* tundra subgroup.

STAND NO.	1	2	3	4	5	6	7
ALTITUDE (m x 10)	229	213	226	229	235	235	235
ASPECT & DEGREE SLOPE	SE7	0	NE3	0	SE4	W2	0
DWARF SHRUBS							
Cassiope tetragona	.	+.03	+.04	.	.	.	.
Dryas octopetala	6.80	5.60	6.99	3.46	13.87	1.13	5.90
Empetrum nigrum	.	.	P	.	.	.	.
Phyllodoce glanduliflora	.	1.03	P	.	.	.	.
Picea engelmannii	.	.	P	.	.	.	.
Salix arctica	1.07	2.50	+.04	.	.	.	.
Salix nivalis	2.47	3.60	1.60	+.25	5.87	2.93	4.80
Sibbaldia procumbens	.	+.07	.	.	.	.	.
Vaccinium vitis-idaea	.	+.03	4.99	2.58	.	.	.
GRAMINOIDS							
Agrostis variabilis	.	+.40	.	.	.	.	.
Carex albonigra	.	+.13	P	.	+.03	+.07	+.07
Carex nardina	.	.	.	.	.	.	+.33
Carex phaeocephala	+.23	.	.	.	.	.	.
Festuca brachyphylla	1.93	1.63	+.20	.	+.30	+.07	+.13
Hierochloe alpina	.	+.07	P	+.04	+.03	.	+.10
Luzula spicata	+.60	+.07	+.20	.	+.37	+.07	P
Poa grayana	+.23	+.07	P	+.21	+.07	+.03	P
Trisetum spicatum	.	+.13	P	+.04	P	.	+.13
FORBS							
Androsace septentrionalis	+.03	.	+.04	.	.	.	.
Anemone drummondii	.	.	.	.	.	.	P
Antennaria alpina/umbrinella	+.17	+.50	+.04	+.08	+.20	+.07	+.17
Antennaria lanata	1.77	+.07	.	.	P	.	.
Arenaria obtusiloba	1.77	+.10	+.28	.	+.10	.	.
Arenaria rubella	.	.	+.16	.	.	+.07	+.03
Arnica alpina	.	.	.	.	.	.	P
Artemisia norvegica	7.90	2.57	P	.	1.10	.	.
Campanula lasiocarpa	+.37	+.60	+.16	+.13	1.17	.	+.23
Castilleja occidentalis	+.23	.	.	.	.	.	.
Draba incerta	.	.	+.12	.	.	.	.
Draba lonchocarpa	.	+.03	.	.	.	+.03	+.03
Draba sp.	+.07	+.03	.	.	+.07	.	.
Erigeron aureus	2.97	.	.	.	.	.	.
Gentiana glauca	.	+.30	P	.	.	.	.
Oxytropis campestris	.	.	.	.	.	.	+.23

TABLE 15 (cont'd)

STAND NO.	1	2	3	4	5	6	7
Oxytropis podocarpa	.	.	.	.	.	.	+.23
Pedicularis arctica	.	+.07	+.08	.	+.07	.	.
Polygonum viviparum	+.17	+.30	.	.	+.20	.	.
Potentilla diversifolia	1.77	+.20	.	.	.	.	.
Potentilla cf. *nivea*	.	.	.	.	+.03	+.03	+.13
Potentilla uniflora	.	.	+.04	.	.	.	.
Saxifraga bronchialis	.	.	P	.	.	.	+.03
Saxifraga caespitosa	.	.	.	.	.	P	.
Sedum stenopetalum	+.50	.	P	.	P	.	.
Selaginella densa	+.57	.	.	.	1.40	.	+.33
Silene acaulis	+.07	.	P	.	+.17	.	.
Solidago multiradiata	.	.	.	.	.	.	+.03
Stellaria longipes	+.03	.	.	.	.	.	.
HEPATICS							
Anastrophyllum minutum	.	P	.	.	.	.	.
Cephalozia sp.	P	.	.	+.04	.	.	.
Cephaloziella sp.	.	P	.	+.13	.	+.13	.
Gymnomitrium corallioides	.	1.57	1.20	.	+.10	.	+.17
Lophozia sensu lato[1]	+.13	+.37	+.16	+.21	+.17	+.17	.
Ptilidium ciliare	.	.	+.08	.	.	.	.
MOSSES							
Amblystegium serpens	.	+.07	.	.	.	.	.
Brachythecium sp.	.	.	P	.	.	.	.
Bryum spp.	+.17	1.83	+.20	+.16	+.50	+.30	+.47
Ceratodon purpureus	.	P	.	+.08	2.57	.	.
Conostomum tetragonum	.	+.47	.	.	.	+.13	
Desmatodon latifolius	.	+.03	+.44	.	.	.	.
Dicranoweisia crispula	.	.	+.08	.	.	.	.
Dicranum ?acutifolium	.	.	1.72	+.08	.	.	.
Dicranum scoparium	+.07	+.47	.	+.33	+.03	+.03	+.03
Encalypta rhaptocarpa	.	.	.	.	.	+.03	+.10
Eurhynchium pulchellum	.	.	.	+.04			
Hylocomium splendens	.	.	.	.	.	+.03	.
Mnium blyttii	.	.	.	+.08	+.07	+.17	+.10
Myurella julacea	.	.	1.92	.	.	.	.
Paraleucobryum enerve	.	+.17	.	+.04	.	.	.
Pogonatum urnigerum	.	.	.	.	.	1.47	.
Polytrichastrum alpinum	.	.	.	.	+.43	.	+.60
Polytrichum juniperinum	+.37	2.87	+.60	.	.	.	.
Polytrichum piliferum	1.80	12.97	1.80	1.75	1.73	+.33	+.37
Rhacomitrium cf. *canescens*	.	+.13	.	.	.	.	.
Rhacomitrium lanuginosum	.	.	+.44	+.54	1.37	1.53	.
Rhytidium rugosum	.	.	.	+.13	+.10	P	.
Tortula ruralis	+.43	+.03	+.04	+.13	+.03	+.17	+.03

TABLE 15 (cont'd)

STAND NO.	1	2	3	4	5	6	7
SAXICOLOUS LICHENS							
Alectoria pubescens	.	.	1.52	+.08	3.53	7.97	10.99
Candelariella vitellina	.	.	+.64	.	+.23	+.83	+.80
Cetraria commixta	.	.	1.32	1.89	.	P	.
Cetraria hepatizon	.	.	.	.	+.03	.	.
Haematomma lapponicum	.	.	.	.	.	.	+.13
Hypogymnia intestiniformis	.	.	+.44	2.46	2.50	3.97	1.97
Lecanora cf. *melanophthalma*	.	.	.	.	+.07		
Lecanora polytropa	+.63	+.17	1.99	+.71	2.53	1.99	1.97
Lecanora rupicola	.	.	.	.	.	1.50	+.13
Lecanora sp.	.	.	+.08	.	.	.	P
Lecidea spp.[2]	+.23	+.23	+.80	+.38	.	+.80	1.73
Parmelia cf. *disjuncta*	.	.	+.08	.	.	.	.
Parmelia taractica	.	.	.	.	.	+.23	+.03
Rhizocarpon disporum	.	.	.	.	.	P	.
Rhizocarpon geographicum	+.30	+.07	1.84	+.71	1.70	2.99	3.99
Rhizocarpon macrosporum	.	.	P	.	.	.	+.07
Rhizocarpon sphaerosporum	.	.	.	.	.	P	.
Rhizocarpon sp.	.	.	+.12	.	.	+.03	2.47
Umbilicaria hyperborea	.	.	1.72	+.08	.	2.90	3.99
Umbilicaria proboscidea	.	.	+.12	.	.	P	.
Xanthoria elegans	.	.	.	.	.	.	P
NON-SAXICOLOUS LICHENS							
Alectoria chalybeiformis	.	.	.	.	P	.	.
Alectoria ochroleuca & *A. nigricans*	.	1.17	+.80	1.58	1.53	1.90	1.99
Alectoria vexillifera	.	.	+.16	.	P	.	.
Arthrorhaphis citrinella	.	+.13	+.12	.	.	+.03	+.23
Buellia papillata	+.03	+.10	+.36	+.08	.	P	+.17
Caloplaca jungermanniae	.	+.07	+.12	+.04	.	+.03	+.17
Caloplaca sinapisperma	.	.	+.08	.	.	+.07	+.30
Caloplaca stillicidiorum	.	.	.	.	.	P	.
Candelariella sp.	.	.	+.04	.	.	.	+.13
Cetraria cucullata & *C. nivalis*	+.10	4.97	1.96	+.63	1.90	1.87	1.97
Cetraria ericetorum & *C. islandica*	1.87	1.57	1.92	+.38	.	+.20	+.23
Cetraria tilesii	+.03	P	+.36	+.42	+.60	+.67	1.97
Cladina mitis	1.87	3.97	1.80	1.71	+.47	.	.
Cladonia chlorophaea s.l.	.	P	.	.	.	.	.
Cladonia coccifera/pocillum/pyxidata	+.73	5.90	4.96	1.42	3.83	1.63	1.93
Cladonia cornuta	.	P	.	.	.	.	.

TABLE 15 (cont'd)

STAND NO.	1	2	3	4	5	6	7
Cladonia ecmocyna	2.87	2.67	+.32	1.38	+.13	+.07	.
Cladonia cf. *macrophyllodes*	.	.	.	+.04	.	.	.
Cladonia uncialis	+.17	+.04	+.	.	.	.	.
Cornicularia aculeata	.	.	1.99	+.13	?	+.--	1.43
Dactylina arctica PD+	+.10	+.23	P	1.16	+.40	.	.
Dactylina ramulosa	.	.	1.76	.	P	.	.
Lecanora cf. *castanea*	.	.	+.32	.	.	.	.
Lecanora cf. *verrucosa*	.	.	+.20	+.13	.	.	.
Lecidea glomerulosa	.	.	+.04	.	.	.	.
Lecidea granulosa	.	1.43	.	+.04	.	+.07	+.20
Lepraria membranacea	.	.	+.04	.	.	.	.
Lepraria neglecta	9.93	3.80	+.52	.	3.77	+.07	+.33
Lobaria linita	.	.	.	.	.	P	.
Nephroma expallidum	.	.	P	.	.	.	.
Ochrolechia upsaliensis	.	.	.	.	.	2.47	1.53
Peltigera spp.[3]	+.23	+.07	2.88	+.33	+.20	1.43	.
Pertusaria coriacea	.	.	+.08	.	.	.	.
Pertusaria dactylina	.	.	+.32	+.04	.	.	.
Physconia muscigena	.	P	.	.	.	.	.
Psoroma hypnorum	+.10	P	1.80	+.13	+.10	.	+.03
Rinodina nimbosa	.	.	+.32	.	.	.	.
Rinodina sp.	.	.	.	+.08	.	P	+.03
Solorina crocea	.	.	+.04	.	+.07	+.03	.
Stereocaulon alpinum	1.93	2.83	1.99	2.58	2.67	+.43	+.03
Thamnolia subuliformis	3.53	1.99	1.99	+.71	1.90	+.90	+.93
ROCKS >6cm diam	.	+.03	7.92	+.18	7.57	8.93	25.99
PEBBLES	21.99	5.63	29.99	65.99	35.99	55.97	25.99
MINERAL SOIL	1.27	14.93	1.76	+.33	2.77	2.93	5.97
LITTER	32.99	23.99	36.99	9.83	22.99	4.99	15.99
VASCULAR COVER	19.99	14.99	10.99	5.79	-	4.99	10.99
BRYOPHYTE COVER	2.93	20.99	3.96	2.79	-	3.87	1.99
LICHEN COVER	17.99	29.99	16.99	9.99	-	26.99	34.99

[1] *Barbilophozia hatcheri, Lophozia* spp.

[2] *L. atrobrunnea, L. dicksonii, L.* spp.

[3] *P. malacea, P. rufescens, P. scabrosa, P. spuria*

[4] Here and elsewhere "litter" refers to detached + attached dead organic matter.

PLATE 7. *Dryas octopetala*/lichen community with solifluction terracettes (stand 3), where much of the arthropod-microhabitat relationships were investigated. Note yellowing *Salix arctica* leaves, and some pink *Dryas* leaves (23 Aug 1970).

PLATE 8. *Dryas octopetala*/lichen community at ca. 2500 m. The *Dryas* covers the areas between the boulders, partially blackened by lichens.

considerable proportion of large rocks (Plate 8). Soil development is extremely poor, regosolic profiles predominating (Table 12).

A common feature of *Dryas*/lichen tundra (Plate 7) is solifluction terracettes (Anderson 1967, Hrapko 1970), also called step-like terraces (Drury 1962), pancake terraces (Hrapko 1970), *Dryas*-banked or turf-banked terraces (Benedict 1970). "The terraces form as a result of surficial frost creep, modified by wind and by the restraining influence of the vegetation cover" (Benedict 1970). In the Bald Hills they develop on gentle slopes, and entail flat-topped lobes up to 5 m long and wide, with steep or shallow-faced risers 10-20(-50) cm high. Small hollows and discontinuous shallow grooves delimit adjacent lobes. The top, normally snowfree or very thinly covered in winter, is typically devoid of vascular plants and has ca. 20-40% cover of saxicolous lichens, mainly on the larger pebbles and rocks because these are less susceptible to frost-induced movement. The risers and hollows have a thick plant cover.

There are three plant strata : (1) a sparse upper layer of graminoids and forbs to 15 cm; (2) a prostrate layer of dwarf shrubs and forbs 1-5 cm high; and (3) a ground layer of cryptogams. *Dryas octopetala*, 1-2.5 cm high, is the dominant species. *Salix nivalis* and *Vaccinium vitis-idaea* are other important woody species. Bryophytes, especially *Rhacomitrium lanuginosum* and *Polytrichum piliferum*, are abundant in depressions and on lower portions of risers. Lichens are abundant

in all parts of the habitat, and exceed all other plant groups in cover. Terrace tops have dark brown and black saxicolous species of *Alectoria*, *Cetraria*, *Hypogymnia* and *Umbilicaria* contrasting with greenish-yellow *Rhizocarpon*. In stand 6 they formed a dark tail or "shadow" on the downslope, windward side of old *Dryas* mats. Associated with *Dryas* and other vasculars are fruticose and foliose species of *Cladonia*, *Dactylina*, *Cetraria* and *Peltigera*, along with inconspicuous but diverse crustose forms. *Stereocaulon alpinum*, *Thamnolia subuliformis*, *Cetraria cucullata*, *C. nivalis* and *Cladina mitis* form prominent groupings in micro-hollows.

Dryas octopetala cover in this community type ranges from 1%, of discrete mat islands, through to virtually solid cover. Island mats occur at the physically most hostile end of the habitat range, with extreme wind exposure and/or shifting unstable slope, usually on shale. In intermediate situations, e.g. rocky but stable slopes often of conglomerate, mats form a reticulate network. Vascular plant cover and variety seem greater on conglomerate than on shale substrata (e.g. Table 15, stands 6 & 7). Lichen cover, dispersion and species richness, however, seem comparable on different surfaces (Table 14). Both saxicolous and non-saxicolous lichens may be controlled less by substrate type and microtopography than by general site conditions such as aspect, snow relations, surface stability, and degree of vascular plant cover.

1b. *Dryas octopetala-Arctostaphylos uva-ursi* subtype.

Only one small stand of this type was found, at 2300-

2350 m on a SE-facing slope. The stable rocky surface, abundance of *D. octopetala*, and prominence of lichens indicate close affinity with the *Dryas*/lichen community type. However, conspicuous mats of *Arctostaphylos uva-ursi* cover ca. 15% of the surface. Over a 3-week period in August 1970, this stand had the highest measured mean daily temperatures.

A. uva-ursi also thrived near timberline on a steep, unstable S-facing gully slope along with *Juniperus communis*, *Dryas octopetala* and a few forbs.

2. *Dryas octopetala/Polytrichum piliferum* type
(stand 2, Table 15)

This type seems restricted to the forest-tundra zone, where it occupies level or very gently sloping upland sites that accumulate much less snow than heath vegetation but more than *Dryas*/lichen communities. Shallow brunisolic profiles are characteristic, with moderate subsurface frost action and intense needle-ice action. Up to 50% of the surface may have deflation patches, developed through the combined action of needle ice and wind, the direction of removal eastward. The bare mineral soil is colonized and stabilized to various degrees by *Polytrichum piliferum* and *D. octopetala*. In stand 2, *Dryas* mats covered ca. 40% of the surface, with shale pebbles and *Polytrichum*-stabilized organic matter covering ca. 30% each.

The community has three strata: (1) a thin upper layer, to 20 cm, of graminoids and forbs; (2) *D. octopetala*, 3-4 cm high, as a well-defined middle layer; (3) cryptogams

forming a conspicuous low layer. *Polytrichum piliferum* is a most important colonizer of bare mineral patches, but also occurs in *Dryas* mats. Lichens, especially *Cetraria nivalis*, *Cladina mitis* and *Thamnolia subuliformis*, are common in *Dryas* mats and in micro-depressions.

This community has some floristic affinities with heaths, harboring species such as *Agrostis variabilis*, *Conostomum tetragonum* and a number of the fruticose lichens. The ordination (Fig. 12) sets it nearest the *Cassiope tetragona*/*D. octopetala* communities, but it belongs to the *Dryas* series by virtue of characteristic lichens such as *Cetraria cucullata*, *C. nivalis* and *Thamnolia subuliformis*, the dominant vasculars *Salix nivalis* and *D. octopetala*, and the virtual absence of heaths. It diverges from *D. octopetala*/lichen communities by lacking many saxicolous lichens and by having better soil development.

3. *Dryas octopetala*/moss type.

In one locality I found the unusual combination of deep snow accumulation but relatively rapid meltout. *D. octopetala* and *Salix arctica* mats were dominant. These were invaded by mosses, especially *Hylocomium splendens* and *Hypnum revolutum*, that formed a thick cover through which only leaves and upper parts of the mat stems protruded. The unique habitat and combination of species in the community precluded its treatment as a subtype of another community type.

4. *Artemisia norvegica/Dryas octopetala* type (stand 1, Table 15).

Besides the well-defined *Dryas* community types, there are in some sites combinations of herb meadow and *Dryas* tundra species. Although content and habitat of this community are intermediate, it falls within the *Dryas* tundra subgroup (Fig. 12).

Snowpack is ca. 1 m, the surface is usually shaly, and saxicolous lichen cover is low. The soil has a homogeneous profile of fine shale pebbles. The community is characterized visually by a reticulate cover of *D. octopetala* mats and a *Lepraria neglecta* crust. There are three layers : (1) an open upper layer of graminoids and forbs to 30 cm; (2) a medium layer of *D. octopetala*; and (3) a low layer of lichens and *Salix nivalis*. *Lepraria neglecta* contributes 80% of the lichen cover and is confined to the very slight (1-4 cm, locally more) micro-depressions. Moss cover is low, restricted to cracks between adjacent lumps of *L. neglecta*.

5. Cushion-rosette type (stands 29 & 30, Table 16).

A rather heterogeneous assemblage of plant communities is included here, in a wide range of elevations, aspects, slopes and snow relations. All have : low vascular plant cover (rarely >10%), with appressed forms dominant; absence or relative scarcity of *Dryas octopetala*; high cover of pebbles, rocks and/or boulders, usually unconsolidated; variable lichen cover.

Most stands of this type occupy windswept ridges and

TABLE 16. Percent cover and frequency of plant species in adjacent stands of cushion-rosette tundra.

STAND NO.	29		30	
	cover (%)	frequency (%)	cover (%)	frequency (%)
VASCULAR PLANTS				
Anemone drummondii	+	6	+	1
Arabis lyallii	0.1	7	+	3
Arnica alpina	+	2		
Artemisia norvegica	+	2	0.1	2
Campanula lasiocarpa	+	4	0.1	16
Carex phaeocephala	0.1	10	0.2	9
Cerastium beeringianum	+	1	+	2
Draba incerta			+	3
Draba cf. *lonchocarpa*	+	3		
Eriogonum androsaceum	+	1		
Festuca brachyphylla	0.2	15	0.2	21
Luzula spicata	0.1	3	+	3
Myosotis sylvatica	+	2	+	1
Poa alpina			+	1
Poa cusickii	+	4	+	1
Poa grayana	+	2	+	4
Potentilla diversifolia	1.3	52	1.1	37
Salix nivalis			0.6	7
Sibbaldia procumbens			+	1
Silene acaulis	+	2		
Solidago multiradiata			+	1
Stellaria longipes	+	1		
Taraxacum lyratum			+	1
Trisetum spicatum	+	7	+	7
BRYOPHYTES				
Bryum sp.	+	1	+	2
Ceratodon purpureus	+	1	+	1
Grimmia sp.	+	1		
Hypnum revolutum			+	1
Polytrichum piliferum			+	1
Rhacomitrium sp.	+	1		
Tortula ruralis	+	10	0.1	11
LICHENS				
Buellia papillata	+	1		
Caloplaca sp.			+	1
Candelariella vitellina	+	1		
Cetraria ericetorum	+	2		
Cetraria islandica & C. ericetorum			0.1	6
Cladina mitis	+	1		
Cladonia cariosa			+	0
Cladonia coccifera & C. pocillum	+	5	0.1	7
Dactylina ramulosa	+	3		
Lecanora polytropa	+	13	0.1	58
Lecanora ?rupicola			+	8
Lecidea sp.	0.1	42	0.2	65
Peltigera scabrosa			+	3
Peltigera spuria	+	1		
Psoroma hypnorum	+	1	+	1
Rhizocarpon cf. *geographicum*	+	4	0.3	48
Rhizocarpon cf. *macrosporum*	+	0		
Rhizocarpon sp.			+	2
Rinodina nimbosa	+	0		
Stereocaulon alpinum	+	1		
ROCKS >6 cm diam.	+	1	5.2	68
PEBBLES	95.5	100	87.0	100
MINERAL SOIL	0.5	41	2.2	85
LITTER[1]	0.5	62	0.6	65
MEAN NO. VASCULAR SPECIES	1.18	63	1.24	66
MEAN NO. BRYOPHYTE SPECIES	0.14	11	0.20	13
MEAN NO. LICHEN SPECIES	0.79	52	2.28	86

[1]Here and elsewhere "litter" refers to detached + attached dead organic matter.

NOTE: + <0.05%.

slopes with little snow accumulation, where most vasculars complete their growth and fruiting by mid-July. Some stands (e.g. nos. 29 & 30) occupy sites with moderate snow accumulation, but here the extremely poor water-holding capacity of the gravelly regosol combined with an unstable surface militate against extensive development not only of vasculars but also cryptogams.

Community structure is tristratal : (1) A thin upper layer, 20-30 cm high, has graminoids e.g. *Carex phaeocephala*, *Poa* spp. *Luzula spicata*, and taller forbs e.g. *Potentilla diversifolia*; (2) the middle layer includes most other vascular species, of cushion (e.g. *Silene acaulis*), rosette (*Arenaria obtusiloba*, *Potentilla nivea* s.l.) and loose (*Campanula lasiocarpa*, *Cerastium beeringianum*) habit; (3) the surface layer has cryptogams and some *Salix nivalis*. Saxicolous lichens are more numerous with increasing rock (vs. pebble) cover (e.g. Table 16). Non-saxicolous lichens and bryophytes show a highly contagious distribution, since they are mostly associated with vascular plant clumps.

5b. *Erysimum pallasii-Ranunculus gelidus* subtype.

This entails a low cover of very early-maturing dwarf forbs on rocky and shaly W and SW-facing ridge crests. The characteristic species are the *Erysimum* and *Ranunculus* along with *Potentilla villosa*, *P. nivea*, *Draba lonchocarpa* and *D. incerta*. All are in full bloom by mid-June, and dispersing seed by early July. Associated may be other, later-developing plants typical of xeric tundra sites, e.g. *Silene acaulis*,

Saussurea densa, Crepis nana and *Cerastium beeringianum.*

5c. Vegetation stripe subtype.

Vegetation stripes, 0.5-1 m broad, are confined to a few upper sections of steep W-facing slopes in the Bald Hills. They have a matrix of *Silene acaulis, Potentilla nivea* and some *Dryas octopetala* colonized by a large variety of vasculars and cryptogams.

5d. Polygon subtype.

Level exposed sites, especially those that have some winter snow, may develop patterned ground if there is enough mineral soil. The polygons are mostly 20-40 cm wide, separated by fissures averaging 3 cm deep. Plant cover is usually confined to the region of the grooves, forming discontinuous anastomosing strips. Xeric-site species e.g. *Arenaria obtusiloba, Cerastium beeringianum, Dryas octopetala, Potentilla nivea* and *Pedicularis arctica* occur along with plants characteristic of more mesic sites e.g. *Artemisia norvegica, Sibbaldia procumbens* and *Phyllodoce glanduliflora.*

5e. Cliff-ledge subtype.

West-facing cliffs are generally too dry to support anything but *Grimmia* and some crustose lichens, but east-facing cliffs and outcrops harbor a rich flora. Most species also occur in *Dryas* tundra or forb meadows. A few vasculars e.g. *Artemisia michauxiana* and *Arnica rydbergii* are characteristic of this habitat, or much more abundant here. The cryptogams *Physcia endococcinea, Xanthoria sorediata, Amphidium*

lapponicum and *Orthotrichum rupestre* were only collected here.

6. Lichen tundra type.

All lithic sites with vascular plant cover less than 1% but lichen cover generally more than 10% belong here. A wide range in elevation, microtopography, aspect and slope is subtended. Conglomerate is much more commonly involved than shale, through eroding shale outcrops may have a high cover and variety of lichens. Areas with negligible plant cover (cf. Plate 9) are considered to lack vegetation types.

6b. Boulder-field subtype.

This subtype comprises areas of unconsolidated but stable boulders piled on one another. Where boulders are large and rounded the plant life is exclusively saxicolous lichens, usually with a high cover over most of the surfaces, and fairly high diversity (20-30 species). Where boulders are smaller and wedged over more of their surface area, or where there are flat areas, the community takes on a very different appearance. In addition to rock lichens over the upper rock surfaces, there are cryptogam micro-communities in crevices and on flat, sheltered rocks. Bryophytes are important here, especially *Ptilidium ciliare, Chandonanthus setiformis* and *Rhacomitrium lanuginosum*; the latter forms large polsters that serve as colonization sites for lichens, especially *Cetraria nivalis*.

Debris islands, generally less than 50 m^2, may be found in boulder fields. They support *Salix nivalis* and other

PLATE 9. Centrally in the Bald Hills, looking south. Barren scree slopes predominate; vegetation (the purple network) on the hilltops and ridges is dominated chiefly by *Dryas octopetala*. The small yellow depressions are herb meadows.

vasculars along with a variety of lichens and bryophytes.

There are a few places where boulders are deeply snow-covered. The very late meltout excludes most lichen growth except for some thin, discontinuous films of gray crustose species. Solid carpets of mosses may occupy soil accumulation between boulders.

7. *Kobresia bellardii* type.

Although only a few small stands occur in the Bald Hills, and none were sampled, they must be recognized as part of a distinct community type because of (1) the outstanding dominant and (2) its preeminent position in other mountain areas. A thick cover of pale yellow *Kobresia bellardii* tussocks characterizes this type, on S-facing slopes or ridge crests that accumulate very little snow. The largest community, covering ca. .05 ha, was on a stable, exposed, 25° S-facing slope. In the same stratum with *Kobresia* were small amounts of *Carex rupestris* and forbs characteristic of *Dryas*/lichen tundra. Some cryptogams were present, mostly in *Kobresia*-free patches.

<u>Heath Group</u>

8. *Cassiope tetragona/Dryas octopetala* type
(stands 8-12, Table 17).

Small (0.1-0.5 ha) communities of this type abound at 2100-2250 m, and there are local occurrences to 2500 m. Maximum snowcover is generally less than 75 cm, though to 1.5 m in stand 9 (Table 24, p.133). This, combined with the presence of *Dryas octopetala*, suggests a medial position between

TABLE 17. Percent cover and frequency of plant species in stands and transect segments of the Heath Group.

STAND NO.	8	9	10	11	12	13	14	15	16	17	18	19
ALTITUDE (m x 10)	229	224	216	232	229	229	223	229	230	232	229	229
ASPECT & DEGREE SLOPE	N5	E18	E10	0	N8	N4	N5	E12	W17	S2	N3	N2
DWARF SHRUBS												
Cassiope mertensiana	.	.	.	.	.	.	*11.97*	*15.73*	*27.97*	.	*28.99*	.
Cassiope tetragona	*21.99*	*11.83*	*10.73*	*12.90*	*8.73*	1.25	.	.	.	.	.	.
Dryas octopetala	*4.99*	*6.93*	*5.77*	*+.07*	*5.57*	.	.	.	.	.	.	.
Empetrum nigrum	P	.	P	.	.	.	P	.	.	.	.	.
Luetkea pectinata	.	.	.	.	.	.	.	.	*5.99*	*18.99*	*6.31*	*21.99*
Phyllodoce empetriformis	.	.	.	.	.	.	.	P	.	.	.	.
Phyllodoce glanduliflora	.	*+.10*	*11.60*	*7.50*	*4.43*	*26.99*	*10.99*	*22.99*	*3.30*	*+.11*	*+.19*	3.33
Salix arctica	*+.33*	*5.70*	*4.83*	*4.77*	*2.37*	*1.99*	*2.63*	*2.60*	.	*2.65*	1.50	.
Salix nivalis	*2.67*	*2.27*	*+.20*	*8.99*	*5.87*	*+.25*	*+.10*	.	.	.	.	.
Sibbaldia procumbens	.	.	.	*+.07*	*+.20*	*1.88*	*+.33*	*1.57*	.	3.99	*+.81*	*+.47*
Vaccinium scoparium	.	.	*+.03*	.	.	.	.	.	.	.	.	.
Vaccinium vitis-idaea	*+.78*	.	*2.63*	*+.03*	.	.	.	.	.	.	.	.
GRAMINOIDS												
Agrostis variabilis	.	.	*+.40*	*+.07*	?	*+.13*	.	.	.	.	.	.
Carex nardina	.	.	.	.	.	.	*+.67*	.	.	.	.	.
Carex nigricans & C. pyrenaica	*+.11*	*+.03*	*+.07*	.	1.73	1.99	*+.10*	*1.53*	*2.80*	*9.99*	*1.81*	6.93
Carex phaeocephala	.	*+.03*	*+.03*	.	.	.	.	.	.	.	.	.
Carex spectabilis	.	.	1.20	.	.	*+.25*	*2.57*	*1.53*	*+.17*	*+.22*	*+.06*	*+.27*
Deschampsia atropurpurea	.	.	.	.	.	.	.	*+.17*	*+.43*	*+.55*	*+.44*	1.93
Festuca brachyphylla	*+.56*	*1.87*	*1.63*	1.63	1.63	.	.	*+.03*	.	.	.	.
Hieracium gracile	.	.	.	.	.	.	.	.	1.60	.	*+.06*	*+.13*
Hierochloe alpina	*+.11*	*+.10*	1.50	.	*+.10*	*+.25*	*+.10*	.	.	.	.	.
Juncus drummondii	.	.	.	.	.	.	.	.	*+.13*	*+.77*	*+.13*	*+.60*
Luzula parviflora/wahlenbergii	.	.	.	*+.03*	.	.	.	.	*1.57*	.	*+.31*	1.33
Luzula spicata	*+.33*	.	*+.07*	*1.73*	*+.07*	1.38	.	.	.	.	.	.

TABLE 17 (cont'd)

STAND NO.	8	9	10	11	12	13	14	15	16	17	18	19
Poa alpina	.	.	.	.	.	.	+.03	.	.	.	.	.
Poa grayana	.	+.07	+.10	+.17	+.43	.	.	.	.	.	.	.
?Trisetum spicatum	.	+.10	+.07	+.13	.	.	.	.	.	.	.	.
FORBS												
Antennaria alpina/umbrinella	+.22	+.40	+.20	1.63	+.07	.	.	.	.	+.77	.	.
Antennaria lanata	.	.	.	.	+.13	1.99	+.43	1.90	1.73	2.99	1.99	4.99
Arenaria obtusiloba	.	+.37	+.03	+.23	+.43	.	.	.	.	.	.	.
Artemisia norvegica	+.33	2.80	2.63	1.37	1.50	+.38	+.40	1.20	.	+.33	+.06	.
Caltha leptosepala	.	.	.	.	.	.	.	.	.	+.11	.	.
Campanula lasiocarpa	+.67	+.77	+.77	+.77	+.73	+.38	+.07	+.17	.	.	.	.
Castilleja occidentalis	.	.	.	.	+.03	+.63	+.03	+.07	+.60	+.33	.	.
Epilobium alpinum	.	.	.	.	.	.	.	.	P	.	.	+.20
Erigeron aureus	.	.	.	.	P	.	.	.	.	.	.	.
Erigeron peregrinus	.	.	.	.	.	.	.	.	.	2.77	.	.
Gentiana glauca	+.33	1.33	+.30	+.47	1.43	+.75	+.53	+.50	.	+.22	.	+.07
Hieracium gracile	.	.	.	.	.	.	.	.	P	.	.	.
Lycopodium alpinum	.	.	.	.	.	.	9.70	3.07	.	.	.	+.07
Pedicularis arctica	.	.	+.03	2.83	+.03	.	+.03	+.03	.	.	.	.
Polygonum viviparum	.	.	1.80	1.73	+.27	.	+.17	.	.	+.11	.	.
Potentilla diversifolia	+.11	+.03	+.07	.	.	+.13	+.10	.	.	.	.	.
Ranunculus eschscholtzii	.	.	.	.	.	.	.	.	.	+.22	.	.
Silene acaulis	+.11	.	.	.	.	.	.	.	.	.	.	.
Stellaria longipes	.	+.03	.	.	.	.	.	.	.	.	.	.
Veronica wormskjoldii	.	.	.	.	.	+.13	3.10	.	.	+.77	.	.
HEPATICS												
Anastrophyllum minutum	+.22	P	.	.	.	.	.	.	.	.	.	.
Cephalozia sp.	.	+.03	P	.	.	.	+.03	.	.	.	+.19	.
Cephaloziella spp.	+.22	.	P	.	.	.	.	.	.	.	+.13	.
Gymnomitrium corallioides	.	+.20	P	.	.	.	.	.	.	.	.	.
Lophozia s.l.[1]	+.78	1.73	.	2.80	2.83	1.63	2.80	1.60	2.80	9.99	4.88	3.99
Gymnomitrium concinnatum & Anthelia juratzkana	1.67	.	.	.	.	2.88	+.10	4.73	1.37	.	2.69	+.07
Tritomaria cf. *quinquedentata*	+.11	.	.	.	.	.	.	.	.	.	.	.

TABLE 17 (cont'd)

STAND NO.	8	9	10	11	12	13	14	15	16	17	18	19
MOSSES												
Aulacomnium palustre	.	.	.	.	.	.	.	.	.	1.22	.	.
Bartramia ithyphylla	.	.	.	.	+.13	.	.	.	.	.	.	.
Brachythecium salebrosum	.	.	.	.	.	.	.	.	.	+.33	.	.
Brachythecium sp.	+.11	+.03	.	.	.	.	.	.	P	.	.	.
Bryum spp.	+.67	1.70	+.27	+.43	+.43	+.88	+.50	+.73	+.30	.	1.81	+.13
Ceratodon purpureus	+.11	+.03	.	.	.	.	.	.	.	.	.	+.07
Conostomum tetragonum	+.22	+.10	+.17	1.53	+.10	1.99	+.20	+.57	+.07	+.11	+.38	.
Cynodontium strumiferum	.	.	.	.	+.03	.	.	.	.	.	.	.
Desmatodon latifolius	.	.	.	.	P	.	.	.	.	.	.	.
Dicranum scoparium	3.99	1.77	6.99	.	2.73	6.99	2.43	5.70	+.30	.	3.75	+.33
Dicranum scoparium & *Kiaeria starkei*	.	.	.	.	.	.	.	.	.	13.88	.	.
Drepanocladus uncinatus	.	.	.	.	.	+.25	+.03	.	1.40	12.77	1.94	+.33
Eurhynchium pulchellum	+.22	.	.	.	.	.	.	.	.	.	.	.
Kiaeria starkei	.	.	.	.	.	.	.	.	9.97	.	6.50	16.99
Kiaeria starkei & *Ditrichum flexicaule*	.	.	.	.	.	.	8.77	.	.	.	.	.
Paraleucobryum enerve	+.11	+.33	+.03	.	1.47	+.25	1.20	+.03	.	+.22	+.06	.
Plagiothecium denticulatum	+.11	.	.	.	.	.	.	.	+.03	.	.	.
Pohlia cruda	+.--	.	.	.	.	+.--	.	.	.	.	+.--	+.--
Polytrichastrum alpinum/ lyallii	.	+.73	4.87	3.87	P	+.88	1.74	+.60	+.77	+.33	+.75	+.87
P. alpinum var. *septentrionale*	.	.	.	.	.	.	.	.	.	.	+.06	+.07
Polytrichum commune	.	.	.	.	+.	.	.	.	.	+.22	.	.
Polytrichum juniperinum	.	.	.	+.07	+.10	.	.	.	.	.	.	.
Polytrichum piliferum	1.99	2.83	6.73	+.17	3.83	+.50	+.13	+.50	+.53	.	+.31	+.33
Lescuraea radicosa	.	.	.	.	.	.	.	.	.	.	+.13	+.20
Rhacomitrium heterostichum	.	.	P	.	+.10	.	.	.	+.17	1.22	.	.
Rhacomitrium lanuginosum	+.44	.	.	.	.	.	.	.	.	.	.	.
Rhacomitrium canescens	.	+.10	.	.	.	.	.	.	.	.	.	.
Rhytidium rugosum	.	.	.	.	+.10	.	.	.	.	.	.	.
Tortula ruralis	.	+.	.	+.	1.	.	+.	.	.	.	.	.

TABLE 17 (cont'd)

STAND NO.	8	9	10	11	12	13	14	15	16	17	18	19
SAXICOLOUS LICHENS												
Lecanora polytropa	.	+.57	.	+.33	+.10	.	+.13	+.03	+.20	.	.	.
Lecanora rupicola	.	.	.	.	+.03	.	+.03	.	.			
Lecidea atrobrunnea	.	.	.	.	+.03	.	.	.	.	.	.	.
Lecidea spp.	.	+.17	+.07	+.30	+.17	.	.	+.03	+.07	.	.	.
Rhizocarpon geographicum	+.11	.	+.03	+.27	1.43	.	+.10	.	+.13	.	.	.
Rhizocarpon sp.	.	+.03	.	.	.	.	.	.	.	.	.	.
Umbilicaria hyperborea	.	.	.	.	1.17	.	.	.	.	.	.	.
NON-SAXICOLOUS LICHENS												
Arthrorhaphis citrinella	.	.	.	.	.	.	.	.	+.03	+.11	.	.
Buellia papillata	+.22	.	+.07	.	+.23	.	.	+.03	.	.	.	.
Cetraria cucullata & *C.* ***nivalis***	3.89	+.07	1.33	+.13	+.17	.	.	.	.	.	.	.
Cetraria ericetorum & *C. islandica*	1.78	2.99	4.97	5.99	3.97	1.99	3.93	2.87	2.57	1.55	1.75	1.60
Cladina mitis	3.99	1.90	10.93	2.99	2.93	4.99	2.60	3.57	.	1.66	+.31	+.07
Cladonia chlorophaea	.	.	.	.	.	.	.	.	P	.	.	.
Cladonia coccifera/pyxidata/ pocillum	2.89	1.99	2.93	2.87	2.99	2.99	1.93	1.80	+.50	1.55	+.63	+.60
Cladonia cornuta	+.11	.	.	.	.	.	.	.	.	.	.	.
Cladonia decorticata	.	.	.	.	.	.	.	.	.	1.33	.	.
Cladonia deformis	.	.	P	.	.	.	.	.	P	.	.	.
Cladonia ecmocyna	3.89	3.97	3.73	1.80	4.99	3.88	2.93	2.87	+.17	1.77	1.81	+.93
Cladonia cf. *macrophyllodes*	+.11	.	.	.	.	.	.	.	.	.	.	.
Cladonia phyllophora	.	.	P	.	.	.	.	.	.	.	.	.
Cladonia uncialis	+.11	.	.	.	.	.	.	+.07	.	.	.	.
Dactylina arctica PD+	+.56	1.67	2.80	1.47	+.43	.	.	.	.	.	.	.
Lecanora castanea	+.11	.	.	.	.	.	.	.	.	.	.	.
Lecidea granulosa	+.11	+.13	+.13	.	+.07	.	+.03	+.13	+.17	.	.	.
Lepraria membranacea	.	.	.	.	.	.	.	.	.	.	.	+.07
Lepraria neglecta	+.33	2.83	3.70	19.97	16.99	3.99	4.90	3.83	8.97	.	1.69	2.87
Ochrolechia cf. *geminipara*	3.78	.	.	.	.	.	.	.	.	+.33	.	.

TABLE 17 (cont'd)

STAND NO.	8	9	10	11	12	13	14	15	16	17	18	19
Peltigera aphthosa	1.44	.	+.13	.	.	+.25	.	.	.	.	2.38	+.07
Peltigera malacea & P. spuria	+.22	.	.	.	.	+.38	.	.	.	.	+.25	.
Peltigera rufescens	.	.	.	.	.	.	.	.	.	2.88	.	.
Peltigera spp.	.	2.93	.	2.70	1.50	.	1.37	+.03	.	.	.	.
Pertusaria dactylina	.	.	.	.	.	+.13	.	.	.	.	.	.
Physconia muscigena	.	.	.	.	.	+.13	.	.	.	.	.	.
Psoroma hypnorum	.	+.37	+.07	+.03	+.03	.	.	.	.	+.11	.	.
Rinodina sp.	.	.	P	.	.	.	.	.	.	.	.	.
Solorina crocea	.	1.40	.	+.07	+.30	+.13	1.17	+.10	+.17	+.11	1.38	1.93
Stereocaulon alpinum	2.99	4.83	3.47	3.97	1.90	1.50	+.03	1.57	.	2.77	+.25	+.20
Thamnolia subuliformis	+.67	+.10	+.17	.	+.23	.	.	.	.	.	.	.
ROCKS >6cm diam.	.	+.03	+.03	1.03	7.47	.	1.13	+.03	2.30	.	.	.
PEBBLES	5.78	5.99	+.03	7.90	+.20	.	+.17	+.07	+.17	.	.	.
MINERAL SOIL	12.78	2.80	6.90	11.99	7.93	3.50	2.77	1.30	1.40	.	+.19	+.07
LITTER	32.99	28.99	28.99	29.99	26.99	48.99	30.99	47.99	45.99	30.99	39.99	36.99
VASCULAR COVER	25.99	32.99	-	-	-	35.99	39.99	42.99	38.99	36.99	39.99	43.99
BRYOPHYTE COVER	6.99	12.99	-	-	-	8.99	19.99	12.99	16.99	38.99	18.99	22.99
LICHEN COVER	17.99	23.99	-	-	-	13.99	13.99	15.99	12.99	9.99	7.99	4.99

[1] *Barbilophozia hatcheri, Lophozia* spp.

xeric tundra dominated by *D. octopetala* and lichens, and mesic tundra dominated by *Phyllodoce glanduliflora* and *Cassiope mertensiana*. The ordination (Fig. 12) supports this view.

On E-facing slopes, the prevailing aspect, *Cassiope tetragona/D. octopetala* communities occupy the slightly raised portions, generally 0.5 m above the *Phyllodoce-Cassiope mertensiana* matrix. The surface is level or irregularly hummocky with a 10-20 cm microrelief, and some large rocks may be present. Soils vary from coarse regosols to ill-defined brunisols. There may be large numbers of small deflation patches, kept under partial control by *Polytrichum piliferum* and films of crustose lichens. Burrows, probably of the Columbian ground squirrel, occur in some stands.

There are four strata : (1) a thin layer of "emergents" to 20 cm tall, formed by *Artemisia norvegica* and graminoids; (2) *Cassiope tetragona*, the aspectual and probably ecological dominant (Plate 10), forming a distinct layer at 10-15(-20) cm of discrete clumps in a canopy cover of 20-30%; (3) a low layer of dwarf shrubs occupying the openings between *C. tetragona* clones. *Dryas octopetala* is the most abundant, with leaves at 3-4 cm; *Salix nivalis* is less than 1 cm high; *Salix arctica* extends into the *C. tetragona* clumps where its stems may reach upward 12 cm or more whereas in the open it is no taller than 7 cm. There is also a small cover of herbs. (4) Cryptogams form the lowest layer. Patches of lichens, 2-3 cm thick, are common, dominated by *Stereocaulon alpinum*, *Cladina mitis*, *Cetraria ericetorum*, *Cladonia coccifera*/

PLATE 10. *Cassiope tetragona/Dryas octopetala* community (stand 10). The heath gives this community type its characteristic brown color. Note yellowing *Salix arctica* leaves.

pyxidata, and *C. ecmocyna*. In some communities *Lepraria neglecta* covers up to 30% of the surface in a lumpy microrelief of 1-3 cm. Bryophyte cover is ca. 10%, mostly *Dicranum scoparium* and *Lophozia* spp. in micro-hollows, and *Polytrichum piliferum* and *Polytrichastrum alpinum* in unstable microsites.

Total vascular plant cover is ca. 30% of which more than 90% is made up of *Dryas octopetala, Cassiope tetragona*, and the two *Salix* species.

Where relief is more pronounced, micro-rises are occupied by *C. tetragona* and *D. octopetala*, and the depressions by *Artemisia norvegica* and even snowbed species such as *Antennaria lanata*. The E sides of hummocks may have some *Vaccinium vitis-idaea*. Mosses are most abundant on the lowest part of the E sides of hummocks.

8b. *Cassiope tetragona-Phyllodoce glanduliflora* subtype (stands 10-12, Table 17).

Some heath areas are transitional between *Cassiope tetragona/Dryas octopetala* and *Phyllodoce glanduliflora-Cassiope mertensiana* communities. Stands 10-12 are identified with the *C. tetragona/D. octopetala* community type through its overall vegetational similarity (Appendix x) and proximity on the ordination field (Fig. 12).

Cassiope tetragona clones, 5-8 cm high, form a conspicuous and homogeneous upper layer. *Phyllodoce glanduliflora* clones, 3 (exceptionally to 7) cm high, are irregularly scattered about. *Salix arctica* (3 cm) and *S. nivalis* (1 cm) form an important lower layer. Rare emergents

of *Artemisia norvegica* and grass culms reach 25 cm. Lichen cover is fairly high, especially of *Lepraria neglecta*. *Stereocaulon alpinum* is conspicuous in some micro-depressions. Bryophytes are less conspicuous, but *Dicranum* and *Polytrichum* can be fairly abundant. Deflation patches are colonized by cryptogams along with some vascular species such as *Luzula spicata*, *Festuca brachyphylla*, *Campanula lasiocarpa* and *Salix* spp.

8c. *Lepraria neglecta* subtype (stand 26, Table 18, p.100).

On the ordination field (Fig. 12) stand 26 lies near the *Cassiope tetragona/Dryas octopetala* group. Many species are common to both, the major difference being the absence of *C. tetragona* in stand 26.

Small patches of this subtype, 1-100 m^2, occupy slight depressions on N and E-facing slopes surrounded by heath tundra, or in rocky uplands where pockets of fines have accumulated. Stand 26 covered ca. .05 ha and was the largest in the Bald Hills.

The ground surface is flat or gently hummocky, with some deflation patches and some wind-deposited shale fragments. Soils are coarse regosols or ill-defined brunisols with relatively high silt content (Table 12).

The outstanding vegetational feature is a whitish surface crust of *Lepraria neglecta*. It forms a lumpy microrelief of ca. 5 cm, and has a cover normally greater than 25% and locally approaching 100%. Associated are a well-dispersed

group of lichens including *Cetraria ericetorum*, *Cladonia ecmocyna*, *C. coccifera*, *Solorina crocea*, *Stereocaulon alpinum*, *Nephroma expallidum* and *Lobaria linita*, and bryophytes including *Barbilophozia hatcheri*, *Bryum* sp., *Pogonatum alpinum* and *Polytrichum piliferum*. Some of these are abundant only along cracks between adjacent "tiles" of the *Lepraria* crust.

9. *Phyllodoce glanduliflora-Cassiope mertensiana* type (stands 13-16,18, Table 17).

Large areas from timberline to 2300 m and locally to 2400 m are dominated by *Phyllodoce glanduliflora* and *Cassiope mertensiana* (Appendix 4), mainly on N and E aspects, but also on W and S aspects where snow accumulation is deep enough (2-3 m late-winter snowpack). The surface is usually slightly hummocky, with a 10-15 cm relief of micro-terraces or pseudo-terraces on most slopes. Some deflation patches, 1-5 (very rarely 10) dm^2, are usually present. These are slightly depressed areas of bare, level mineral soil, sometimes with a veneer of small pebbles. Shale fragments, evidently blown in, may cover up to 10% of the stand surface. The soil is immature but shows a better developed dystric brunisol profile than the earlier types (Table 12). Ground squirrel burrows occur in some of the stands.

Two low shrubs, *Phyllodoce glanduliflora* and *Cassiope mertensiana*, dominate in a combined cover of 15-50%. Toward timberline *Vaccinium scoparium* and *Phyllodoce empetriformis* assume some importance. The two dominants usually form a closed canopy a uniform 5-7 cm high with flower stalks to 9

cm. In communities with earlier snow release the *P. glanduliflora* is up to 10 cm high. It has fairly open growth, the branches farther apart and tending toward the horizontal, whereas *C. mertensiana* has a dense erect habit. In contrast to *Cassiope tetragona*, *C. mertensiana* is shorter and exhibits dense continuous growth rather than well spaced clumps.

Vascular plants at three levels provide 10-15% cover: (1) a sparse "emergent" layer, to 25 cm, of graminoid culms mainly of *Carex spectabilis* and *C.* cf. *pyrenaica*, and flower stalks to 15 (exceptionally 20) cm, of *Antennaria lanata* and *Artemisia norvegica*; (2) forb leaves, mostly of the previous two, conforming to the heath height; (3) a layer of *Salix arctica* at 3-5 cm, and a very low layer of *Sibbaldia procumbens*. *Lycopodium alpinum* is important in some communities, forming narrow, dense clones 2-3 cm high and up to several meters long. Some clones form rings to 2 m or more in diameter, with only the outermost 20-30 cm live, dying back in a conspicuous band of yellowish-white stems.

The cryptogam layer is well developed and homogeneous (cf. low ratio of standard deviation : mean cover in Table 14), with bryophytes and lichens about equally important. Members of the Dicranaceae form much of the moss cover. They are not conspicuous but fairly abundant, especially in micro-hollows and along the E side of hummocks. Lichen cover is dominated by species of *Cladonia*, *Cetraria* and *Cladina*, mainly in the many little openings between heath clone aggregations. *Lepraria neglecta* is also important, especially as a stabilizer

of deflation patches, and creates a bumpy microrelief of 3-6 cm. Cryptogam micro-communities are common, with *L. neglecta* and *Conostomum tetragonum* on tops of tiny (5 cm) mounds, *Lophozia* on the sides and in cracks, and bits of *Bryum* and other bryophytes on the bottom sections.

9b. *Phyllodoce glanduliflora* subtype (stand 13, Table 17).

In the Bald Hills, the two dominants of the *Phyllodoce-Cassiope mertensiana* type occur together much more often than they do apart. I have considered sites where *P. glanduliflora* is the sole dominant as transitional between *Cassiope tetragona/D. octopetala* and *Phyllodoce-Cassiope mertensiana* communities but nearer the latter (cf. Fig. 12), and have relegated them to subtype status. Aside from the dominant species, there seem to be no other distinctive features to this subtype.

9c. *Cassiope mertensiana* subtype (stand 18, Table 17).

C. mertensiana as the sole dominant occupies large areas in the headwaters area of Evelyn Creek, and small stands in the N half of the Bald Hills. The surface is usually more hummocky than that of *Phyllodoce-Cassiope* communities. There are more snowbed species e.g. *Antennaria lanata, Deschampsia atropurpurea* and *Epilobium alpinum*, and total vascular cover is high (40-70%). *A. lanata* and *Carex nigricans* may form a rather dense cover in depressions (20-30 cm). Mosses are not conspicuous but form a 1-2 cm cover of 20-25%. *Kiaeria starkei* and *Barbilophozia hatcheri* are the most abundant,

forming solid masses on N-facing sides of hummocks. *Polytrichastrum* stems are dotted about in heath-free patches, and lichens are confined mainly here. *Polytrichum piliferum* and hepatics cover stabilized deflation patches.

10. *Luetkea pectinata* type (stands 17 & 19, Table 17).

Luetkea occupies the deepest-snowpack portion of the Heath Series. The substrate is usually moist through the season, though not necessarily cool, viz. stand 16 (Table 17) on a steep W-facing slope. The surface is generally micro-hummocky, and sometimes concave. Soil silt content appears higher here (30-45%) than in the rest of the heaths (20-25%).

Luetkea forms a variably dense but fairly uniform cover 2 cm high with scapes to 5 cm. *Cassiope mertensiana*, scarcely higher, forms an irregular (in deeper snowbeds) or fairly uniform cover, or is absent. Conspicuous emergents include *Deschampsia atropurpurea* at 15-20 cm, and *Antennaria lanata* at 4-5 cm with scapes to 12 cm. Other species are drawn from Heath Tundra and Forb Meadows but do not form a high cover.

The high bryophyte cover is similar in composition to that in the *Cassiope mertensiana* subtype. Lichen cover is very low.

<u>Herb Meadow Group</u>

11. *Artemisia norvegica/Salix arctica* type (stand 21, Table 18).

Small communities of this type occupy gentle slopes, mostly N & E-facing, from below timberline to ca. 2250 m.

TABLE 18. Percent cover and frequency of plant species in stands and transect segments of the Herb Meadow (nos. 20-25) and Snowbed (nos. 27-28) Groups.

STAND NO.	20	21	22	23	24	25	26	27	28
ALTITUDE (m x 10)	232	213	223	223	229	232	232	223	229
ASPECT & DEGREE SLOPE	S2?	N5	0	E35	E16	E20	N17	E15	N1
DWARF SHRUBS									
Cassiope mertensiana	.	.	+.03	.	.	2.13	.	+.10	.
Dryas octopetala	.	.	.	.	.	.	+.10	.	.
Luetkea pectinata	.	.	+.17	.	.	.	.	.	+.33
Phyllodoce empetriformis	.	.	+.13	+.03	.	.	.	.	.
Phyllodoce glanduliflora	+.11	.	.	1.03	.	.	.	+.10	.
Salix arctica	8.99	9.90	8.93	.	.	.	7.70	.	.
Salix nivalis	.	.	.	.	.	.	+.07	.	.
Vaccinium caespitosum & *V. scoparium*	.	3.70	1.10	P	.	.	.	.	.
GRAMINOIDS									
Agrostis variabilis	+.11	.	+.30	.	.	.	.	.	.
Calamagrostis inexpansa	.	+.07	.	.	.	.	.	.	.
Carex atrata	.	P	.	.	.	.	.	.	.
Carex brunnescens	.	.	+.13						
Carex nigricans & *C. pyrenaica*	1.55	+.37	2.43	11.97	4.60	3.87	+.27	57.99	74.99
Carex spectabilis	1.77	2.57	6.97	2.57	4.76	2.87	1.03	.	.
Deschampsia atropurpurea	1.77	.	.	1.60	.	+.03	.	+.53	2.67
Deschampsia cespitosa	.	1.30	.	.	.	.	.	.	.
Festuca brachyphylla	1.11	+.37	1.53	.	+.13	.	+.60	.	.
Hierochloe alpina	.	+.17	.	.	.	.	.	.	.
Juncus drummondii	+.88	.	+.07	P	.	P	.	+.13	.
Luzula parviflora	.	.	6.67	2.73	+.23	1.20	.	5.67	.
Luzula spicata	+.11	+.07	+.07	.	.	+.10	+.50	.	.
Luzula wahlenbergii	.	.	+.03	.	.	.	.	.	.
Phleum alpinum	+.22	+.10	2.73	1.20	.	1.10	.	+.07	.
Poa alpina	.	+.03	.	.	+.10	+.13	+.03	.	.
Poa cusickii	+.11	+.33	+.37	1.57	+.23	1.80	.	P	.
Poa grayana	.	+.03	+.13	+.13	+.30	.	+.47	+.33	.
Trisetum spicatum	.	.	+.03	+.13	.	.	+.03	+.10	.
FORBS									
Agoseris aurantiaca	.	+.37	+.03	+.13	.	1.33	.	.	.
Androsace septentrionalis	.	.	.	.	P	.	.	.	.
Anemone occidentalis	.	.	.	12.93	.	P	.	+.07	.
Antennaria alpina/umbrinella	.	.	1.10	.	.	.	+.30	+.03	.
Antennaria lanata	5.99	1.33	4.90	7.77	7.87	8.97	+.10	+.07	.
Arabis lyallii	.	.	.	.	+.23	+.03	.	.	.
Arabis lyrata	.	P	.	.	.	.	.	.	.
Arenaria obtusiloba	+.11	.	+.10	.	+.03	+.13	1.80	.	.
Arnica alpina	.	.	.	.	P	.	.	.	.
Arnica diversifolia	.	.	.	.	P	P	.	.	.

TABLE 18. (cont'd)

STAND NO.	20	21	22	23	24	25	26	27	28
Arnica mollis	.	1.13	.	2.27	3.53	4.63	.	.	.
Arnica rydbergii	.	.	.	.	P	.	.	.	.
Artemisia norvegica	1.44	17.83	15.87	4.70	11.90	6.80	2.83	+.03	.
Caltha leptosepala	.	2.47	.	.	.	.	.	.	.
Campanula lasiocarpa	.	.	.	+.13	+.37	+.33	+.93	+.03	.
Cardamine oligosperma	.	.	.	+.13	.	.	.	.	.
Castilleja occidentalis	1.77	+.03	+.13	1.37	+.03	2.43	.	.	.
Castilleja rhexifolia	.	P	.	.	.	.	.	.	.
Claytonia lanceolata	.	.	.	.	.	P	.	.	.
Draba lanceolata	.	.	.	.	.	+.07	.	.	.
Draba lonchocarpa	.	.	.	+.17	.	.	+.10	.	.
Draba sp.	.	.	.	.	.	.	+.07	.	.
Epilobium alpinum	.	+.07	.	+.77	.	+.23	.	1.70	–
Erigeron peregrinus	1.77	3.73	+.10	+.07	1.33	1.50	.	+.03	+.17
Gentiana glauca	+.22	+.03	+.03	.	.	.	.	.	.
Gentiana propinqua	.	P	.	.	.	.	.	.	.
Hieracium gracile	.	+.07	.	+.27	+.03	+.13	.	+.03	.
Lycopodium alpinum	.	.	.	+.03	.	.	.	.	.
Pedicularis bracteosa	.	+.03	.	P	.	.	.	.	.
Pedicularis groenlandica	.	+.07	.	.	.	.	.	.	.
Polygonum viviparum	.	1.53	.	.	.	.	.	.	.
Potentilla diversifolia	+.22	4.93	1.33	+.03	1.33	+.03	+.07	.	.
Ranunculus eshscholtzii	.	+.43	+.03	+.53	1.23	+.30	.	.	.
Sedum stenopetalum	.	.	.	.	+.10	+.27	.	.	.
Selaginella densa	.	.	.	.	.	3.70	.	.	.
Senecio pauciflorus	.	+.20	.	+.03	.	.	.	.	.
Senecio triangularis	.	2.43	.	5.73	.	.	.	+.07	.
Sibbaldia procumbens	6.99	1.50	9.93	1.47	4.63	5.83	1.53	+.03	.
Silene acaulis	.	.	.	.	.	.	+.07	.	.
Solidago multiradiata	.	1.17	.	.	.	.	.	.	.
Stellaria longipes	.	+.50	+.13	.	.	.	.	.	.
Trollius laxus	.	3.33	.	.	.	.	.	.	.
Valeriana sitchensis	.	P	.	.	.	.	.	.	.
Veronica wormskjoldii	+.55	1.90	+.43	1.70				+.17	
HEPATICS									
Blepharostoma trichophyllum	.	P	.	.	.	.	.	.	.
Cephalozia media	.	+.07	.	.	.	P	.	.	.
Cephaloziella sp.	.	.	P	P	.	.	.	.	.
Lophozia s.l.[1]	.	1.63	4.93	6.87	+.07	+.13	2.87	+.27	.
?*Orthocaulis* sp.	.	.	.	P	.	.	.	.	.
Scapania irrigua	.	+.03	.	+.03	.	.	.	.	1.17
Tritomaria sp.	.	P	.	.	.	.	.	.	.

TABLE 18 (cont'd)

STAND NO.	20	21	22	23	24	25	26	27	28
MOSSES									
Amblystegium serpens	.	.	.	+.57	+.10	+.03	.	.	.
Aulacomnium palustre	.	15.97	20.93	+.07	.	.	.	.	.
Bartramia ithyphylla	.	.	.	P	.	.	.	.	.
Brachythecium salebrosum	.	5.67	+.20	+.10	1.33	.	.	.	.
Brachythecium turgidum	.	+.03	1.23	.	.	.	.	.	.
Brachythecium cf. *velutinum*	.	.	.	.	.	.	+.07	.	.
Brachythecium sp.	.	+.03	.	+.37	P	+.27	.	.	.
Bryum pseudotriquetrum	.	+.20	+.03	P	.	.	.	.	.
Bryum spp.	1.11	+.10	+.17	1.43	+.27	+.30	1.87	+.03	.
Ceratodon purpureus	.	.	.	+.07	.	.	.	.	.
Cirriphyllum cirrosum	.	.	.	+.10	.	.	.	.	7.97
Conostomum tetragonum	.	.	.	+.03	.	.	.	.	.
Desmatodon latifolius	.	+.03	.	+.03	.	.	.	.	.
Dicranum scoparium	.	1.47	6.70	P	.	.	.	.	.
Ditrichum flexicaule	.	.	1.10	.	.	.	.	+.07	.
Drepanocladus uncinatus	+.33	.	+.07	+.03	+.03	.	.	.	+.67
Drepanocladus vernicosus	.	4.60	+.17	.	.	.	.	.	.
Encalypta cf. *rhaptocarpa*	.	+.03	.	+.03	P	.	.	.	.
Eurhynchium pulchellum	.	.	.	.	.	.	P	.	.
Grimmia sp.	.	.	.	+.07	.	.	.	.	.
Hylocomium splendens	.	12.93	.	.	.	.	.	.	.
Kiaeria starkei	.	.	.	+.13	.	.	P	+.13	1.17
Paraleucobryum enerve	.	.	.	.	.	.	1.70	.	.
Plagiothecium denticulatum	.	.	.	.	.	.	.	1.20	.
Pohlia cruda	.	.	.	+.03	.	.	.	+.23	.
Polytrichastrum alpinum/ lyallii	.	+.03	+.03	1.70	1.70	1.93	+.47	+.20	1.99
P. a. var. *septentrionale*	.	.	.	.	.	.	.	+.20	.
Polytrichum commune & *P. juniperinum*	1.99	+.50	3.99	2.73	.	.	.	.	.
Polytrichum piliferum	3.44	+.03	+.03	+.07	1.53	+.57	5.93	+.07	.
Lescuraea radicosa	.	.	.	7.93	.	.	.	.	1.17
Rhacomitrium canescens	.	+.03	.	.	+.10	+.07	+.17	.	.
Tortella tortuosa	.	+.10	.	.	.	.	.	.	.
Tortula norvegica	.	.	+.07	1.53	.	.	+.03	.	.
Tortula ruralis	.	.	.	+.07	.	.	+.10	.	.
Tortula norvegica & *T. ruralis*	.	.	.	.	+.37	+.50	.	.	.
LICHENS									
Buellia papillata	+.22	.	.	.	+.03	+.03	+.27	+.27	.
Candelariella vitellina	.	.	.	+.03	.	.	.	.	.
Caloplaca sinapisperma	.	+.03	.	.	.	.	.	.	.
Cetraria islandica & *C. ericetorum*	1.77	+.17	+.17	+.07	1.60	1.63	2.87	.	.

TABLE 18 (cont'd)

STAND NO.	20	21	22	23	24	25	26	27	28
Cetraria nivalis	.	+.03	.	+.07	.	.	+.07	.	.
Cladina mitis	4.99	+.07	+.10	+.20	.	.	+.40	.	.
Cladonia cariosa	.	.	.	.	+.03	.	.	.	.
Cladonia chlorophaea s.l.	.	.	+.03	+.13	.	.	.	.	.
Cladonia coccifera & C. pyxidata	1.77	.	+.20	.	P	+.10	1.90	.	.
Cladonia ecmocyna	2.99	+.23	+.37	+.33	4.80	1.67	4.97	+.07	.
Cladonia macrophyllodes	.	+.03	.	+.03	.	.	.	.	.
Cladonia pleurota	.	.	+.03	.	.	.	.	.	.
Dactylina ramulosa	.	.	.	.	.	.	+.13	.	.
Lecanora polytropa	.	.	.	+.07	+.17	+.20	+.70	.	.
Lecanora sp.	.	.	.	+.	.	+.	+.	.	.
Lecidea granulosa	+.11	.	+.03	.	+.03	+.03	+.07	.	.
Lecidea sp.	.	.	.	+.03	+.07	+.13	+.70	.	.
Lepraria membranacea	.	.	.	P	.	.	.	.	.
Lepraria neglecta	1.66	.	+.10	+.03	+.03	1.53	26.97	.	.
Lobaria linita & Nephroma expallidum	.	.	.	+.10	.	.	3.80	.	.
Peltigera aphthosa	.	+.10	3.43	P	.	.	P	.	.
Peltigera spp.[2]	6.77	1.23	1.47	3.63	3.67	3.63	.	.	.
Psoroma hypnorum	+.11	.	.	P	+.17	+.07	+.03	.	.
Rhizocarpon cf. *geographicum*	.	.	.	+.13	+.03	+.07	+.33	.	.
Rhizocarpon macrosporum	.	.	.	+.10	.	.	.	.	.
Rinodina sp.	.	.	.	.	P	.	P	.	.
Solorina crocea	+.11	.	.	.	.	.	1.53	+.07	.
Stereocaulon alpinum	1.99	.	1.33	+.10	+.13	+.23	1.87	+.10	.
Thamnolia subuliformis	.	.	.	+.03	.	.	.	.	.
ROCKS >6cm diam.	.	.	.	3.30	.	.	+.03	+.10	.
PEBBLES	.	.	.	+.27	27.97	27.99	24.99	.	.
MINERAL SOIL	.	+.03	+.03	.	1.80	+.13	3.50	.	.
LITTER	34.99	30.99	22.99	32.99	27.99	28.99	17.97	37.99	27.99
VASCULAR COVER	32.99	46.99	53.99	48.99	27.99	35.99	14.99	61.99	74.99
BRYOPHYTE COVER	23.99	47.99	40.99	22.99	3.90	6.99	9.93	10.97	2.99
LICHEN COVER	17.99	1.53	6.83	4.83	9.93	7.90	40.97	+.13	.

[1] *Lophozia* spp, *Barbilophozia hatcheri;* also *B. lycopodioides* in stands 21 & 23.

[2] Mostly *P. rufescens;* also *P. canina, P. horizontalis/polydactyla.*

They melt out fairly early but remain moist most of the season, fed by snowbank meltwater which sometimes dissects the stands with a number of ephemeral streams. The communities are subject to accumulation of fine alluvial sediment, and the soil clay content (20-30%) is 2-3 times that in other Bald Hills communities (Table 12). There are no surface rocks, but the range of microrelief is up to 5 dm inclusive of streambeds. Some stands have small earth or moss hummocks.

The communities are never large since they are related to surface-discharge sites. But they are distinctive in three respects : (1) the duration of vascular plant growth is relatively long, usually three months; (2) there is high vascular plant cover and species richness, high bryophyte cover, and very low lichen cover; (3) there is a characteristic three-stage phenology (Fig. 15) :

a. *Trollius laxus*, *Caltha leptosepala*, *Ranunculus eschscholtzii* and *Salix arctica* bloom in early June.

b. In early to mid-July *Pedicularis* spp. and *Potentilla diversifolia* are in conspicuous bloom together with many less prominent species; *Artemisia norvegica* leaves are very abundant.

c. A burst of flowering in late July-early August, by tall forbs and grasses. In some years the season is too short to allow this, and flowering stalks of *Artemisia* predominate.

This community type is the most unlike of the Herb Meadow Group (Fig. 12, Appendix 5), probably due to the species richness. There are three strata : (1) an upper layer of tall forbs at 25-35 cm and graminoids at 40-50 cm; important species are *Trollius laxus*, *Potentilla diversifolia*,

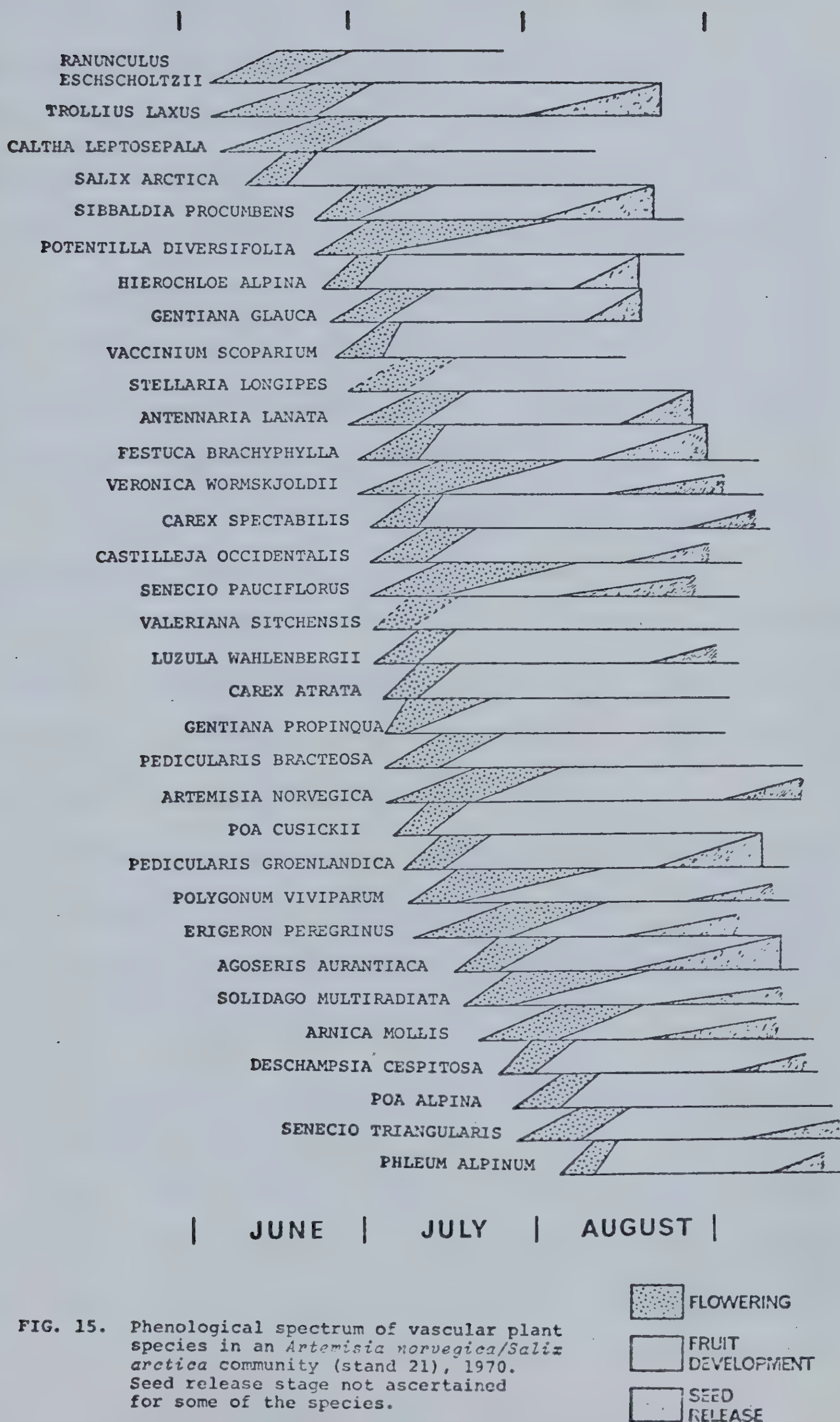


FIG. 15. Phenological spectrum of vascular plant species in an *Artemisia norvegica/Salix arctica* community (stand 21), 1970. Seed release stage not ascertained for some of the species.

Artemisia norvegica, *Erigeron peregrinus*, *Arnica mollis*, *Senecio triangularis*, *Carex spectabilis*, and in some stands *Valeriana sitchensis* and *Castilleja rhexifolia*; (2) a dense layer of vasculars at 5-20 cm, formed chiefly by *Salix arctica*, *Veronica wormskjoldii*, *Solidago multiradiata*, *Caltha leptosepala*, and foliage of the tall forbs especially *Artemisia norvegica*; (3) a luxuriant 4-5 cm thick layer, in places continuous, of bryophytes dominated by *Aulacomnium palustre* and *Hylocomium splendens*. Lichens are confined to small water-eroded bare patches.

Fragments of this community type, generally <50 m^2, occur here and there in the Bald Hills, usually in the vicinity of streamcourses (Plate 11). They have a relatively depauperate flora dominated by a few tall forbs, usually *Arnica mollis* and *Senecio triangularis*. I noted one stand where *Erigeron peregrinus* was the dominant.

Species belonging to the *Artemisia norvegica/Salix arctica* community type, especially *Senecio triangularis*, also occur at the base of solifluction lobes, probably in response to water and nutrient discharge.

12. *Artemisia norvegica-Luzula parviflora* type (stand 22, Table 18).

One stand of this type, 0.5 ha in size, occurs in the Bald Hills (Plate 12). It occupies a very shallow basin with a high water table. The soil profile is unusual in two respects : (1) it is undisturbed, whereas other soil profiles in the study area reflect some degree of frost or gravity-

PLATE 11. Shaly streambed with Herb Meadow fragment. Dominant are robust clumps of *Senecio triangularis* (shiny-leaved) and *Arnica mollis*, two cornucopian species for anthemophilous insects.

PLATE 12. *Artemisia norvegica-Luzula parviflora* community (stand 22). Note the characteristic color of the woodrush. In the background is mostly heath-dominated tundra.

induced movement; (2) it has a pale gray B horizon, probably a product of slope wash.

The community has four strata : (1) an upper layer, at 30 cm, of graminoids. Although it has only 6% cover, *Luzula parviflora* is the phenological dominant of the community, giving it a distinctive dark reddish cast (Plate 12). Other important graminoids are *Carex spectabilis*, *C. nigricans* and *Phleum alpinum*. (2) a diffuse middle layer, mainly at 15-25 cm, of scapes of *Artemisia norvegica*, *Festuca brachyphylla*, *Juncus drummondii* and *Agrostis variabilis*; (3) a well developed leaf layer of *A. norvegica*, *Salix arctica* and *Antennaria lanata* at 7-10 cm, and *Sibbaldia procumbens* close to the surface; (4) a 5 cm thick moss layer dominated by *Aulacomnium palustre*. Lichens, especially *Peltigera* spp. and *Stereocaulon alpinum* , are mostly confined to micro-hollows. The diagnostic features of the community type are the dominance by graminoids in the top stratum, and the high cover of *Aulacomnium palustre*.

13. *Artemisia norvegica-Anemone occidentalis* type (stand 23, Table 18).

Stands of this type cover a very small part of the study area, in the range 2150-2300 m. They are confined to very steep (25-40°) hillsides on NE through SE aspects, with late meltout and a steady moisture supply from upslope snowbanks. They grade into *Carex nigricans* snowbeds at the foot of the slopes.

The soil is a Cumulic Regosol, churned up by frost

action and continual downslope movement. Cave-ins of ground squirrel burrows have resulted in bare mineral patches and overhangs.

There are four strata : (1) scapes and heads of *Anemone occidentalis* (30-40 cm), and a number of slightly shorter forbs particularly *Senecio triangularis*, *Artemisia norvegica* and *Arnica mollis*; also graminoids especially *Phleum alpinum*, *Poa* spp., *Carex spectabilis* and *Luzula parviflora*; (2) a diffuse , 15-20 cm layer of forbs together with *A. occidentalis* foliage; (3) a low leaf layer of *Arnica*, *Antennaria lanata*, and *Carex nigricans/pyrenaica*; (4) a cryptogam layer of numerous bryophyte species. Lichen cover is ca. 5%, mainly *Peltigera* spp.

The phenological and ecological dominants are *Anemone occidentalis*, *Arnica mollis*, *Artemisia norvegica* and *Carex nigricans/pyrenaica*. The best identifying features of the community are its restriction to cool steep slopes fed by snow meltwater, and the abundance of *A. occidentalis*.

13b. *Artemisia norvegica-Anemone occidentalis/Phyllodoce* subtype.

Small communities of this kind occur in the S half of the Bald Hills, on well-watered gentle slopes of all aspects mainly at 2200-2300 m. Although unique in combining forbs and heaths in a dense cover, these communities have obvious floristic affinities with the *Artemisia norvegica-Anemone occidentalis* type.

There are four layers : (1) a thick upper forb layer,

to 40 cm, dominated by *Artemisia norvegica*, *Anemone occidentalis*, *Senecio triangularis* and *Castilleja rhexifolia*; (2) a middle layer, at 5-10 cm, of *Phyllodoce empetriformis* and *P. glanduliflora*; (3) a discontinuous layer of low forbs, e.g. *Veronica wormskjoldii*, *Campanula lasiocarpa* and *Antennaria lanata*; (4) a layer of cryptogams, mainly bryophytes since these are better adapted than lichens to the damp and dark surface microenvironment.

14. *Artemisia norvegica-Antennaria lanata* type (stands 24 & 25, Table 18).

This community diverges from other Herb Meadow types by its pebbly surface and negligible soil development. Representative stands occur on fairly steep E-facing slopes at 2200-2350 m. Downslope pebble movement has resulted in a stepped appearance, level or slightly sloping strips of bare pebbles alternating with "risers" stabilized by plants. Snowmelt is fairly late, and ground water from upslope snowbanks is probably responsible for the relatively high productivity.

There are four layers : (1) at 25-30 cm are *Arnica mollis*, the late-season phenological dominant, and *Artemisia norvegica*, less conspicuous but more abundant; *Carex spectabilis* (30 cm) forms fairly dense patches; (2) a layer of leaves, at 4-8 cm, of *Artemisia*, *Arnica* and *Antennaria lanata*, the latter very conspicuous in mid-season; also, dense patches of *Carex nigricans/pyrenaica*; (3) at 1-2 cm, patches of *Sibbaldia procumbens* and (in stand 25) *Selaginella densa*; (4) a cryptogam layer with 10% cover each of

bryophytes and lichens. Predominant lichen forms are the very appressed (*Peltigera*, primary thalli of *Cladonia ecmocyna*) and loose (*Cetraria*). Colonies of *Polytrichastrum* cf. *lyallii* and *Polytrichum piliferum* characterize the bryophye complement.

The risers of large solifluction lobes support vegetation that most closely approximates this community type's. *Artemisia norvegica* dominates, with *Sibbaldia procumbens* and *Carex spectabilis* strong associates. The latter is especially abundant on lobe faces that have been broken up through burrowing activity of ground squirrels. Thick patches of the sedge are good indicators of ground disturbance.

Snowbed Group

15. *Carex nigricans* type (stands 27 & 28, Table 18).

This type is represented by numerous patches rarely exceeding .02 ha in depressions or concave sections of mostly N & E-aspect slopes. Snow release is in late June - early July. The surface is uniformly hummocky, the microrelief ca. 30 cm. The hummocks typically have a large central silt lens; silt accumulation is greatest in this community type (Table 12).

Stands are easily recognized by the yellowish cast of previous seasons' *Carex nigricans* leaves (Plate 13). This sedge is an outstanding dominant, forming a much denser cover than any other species in the Bald Hills. The bottom 3 cm are particularly dense, thinning to 7 cm, with some leaf tips to 12 cm. Scapes are abundant though not conspicuous, generally 12-17 cm high.

PLATE 13. Telescoped vegetational zonation, with *Dryas octopetala*/lichen tundra at lower right grading directly into *Carex nigricans* snowbed. Beyond is a fringe of *Antennaria lanata* (bluish-gray), some *Phyllodoce glanduliflora* (in flower), and *D. octopetala* mats near ridge crest.

There are three additional strata : (1) a thin but homogeneous "emergent" layer of graminoid scapes : *Deschampsia atropurpurea* at 15-20 cm, *Luzula parviflora* at 35-40 cm, also tufts of *Juncus drummondii* and a few stems of *Phleum alpinum, Trisetum spicatum* and *Poa grayana*; (2) a low layer of evenly dispersed *Epilobium alpinum*; (3) a thin layer of bryophytes which, although impossible to see without parting the *Carex* leaves, form a surprisingly good, even cover. *Cirriphyllum cirrosum* dominated in stand 27. Lichens are extremely scarce.

In the community type's nodal or optimal expression, these are the only plants. *Senecio triangularis, Arnica mollis*, and a few lichens are common at the stand periphery and sometimes on hummock tops, and indicate slightly earlier snowmelt.

More noteworthy yet is the position of *Antennaria lanata*. This species gets progressively more abundant from xeric to mesic communities in the heath series. Its optimal development seems to be in a constantly recurring 1-3 m wide band between heath and *Carex nigricans* snowbeds (cf. Plate 13). Aspectually it is very prominent due to the numerous pale *A. lanata* leaves.

16. *Luzula* snowbed type.

This type is represented on some very late snowmelt sites with moderately steep N and E-facing slopes of loose shale pebbles. The very short growing season, no more than 6-8 weeks, combined with continual downslope movement of the

surface, preclude any soil development. However, the sheltered site does favor some vascular plants.

The normal pattern consists of regularly dispersed dark red clumps of *Luzula parviflora* and/or *L. arcuata*. Also present may be *L. spicata*, *Carex pyrenaica*, *Cardamine bellidifolia*, *Oxyria digyna*, *Epilobium alpinum* and *Juncus drummondii*. *Silene acaulis*, a typical upland tundra species, may also occur here. There may be some moss clumps, but lichens are very rare. Total plant cover is ca. 5%, rarely approaching 10%.

Moving onto more stable sites of shallower slope and/or a larger increment of conglomerate rock, the *Luzula* snowbed grades into *Carex nigricans*, *Luetkea pectinata*, or *Cassiope mertensiana* communities. There is also a transition to extremely late-lying snowbeds, often hectares in size (Appendix 4), where plant cover is negligible or nil.

17. *Poa cusickii* type.

Several hectares of convex E-facing hillsides (Appendix 4) are covered with loose shale pebbles. Upslope moisture sources are lacking, which leads to drought conditions soon after the rather late snowmelt. The surface is not particularly active except in gullies, where subject to running-water erosion.

Poa cusickii tussocks provide a very low (ca. 1%) but conspicuous cover. There are rare clones of *Carex nigricans*, *Silene acaulis* and *Arabis lyallii*, and a few loose mats of *Polytrichastrum*. There is virtually no other plant life.

<u>Other community types</u>

18. *Eriophorum polystachion/Calliergon sarmentosum* type.

Communities of this type are found locally from timberline to 2250 m. They occupy level, flat areas that are water saturated all or virtually all season. The soils have a thin layer of organic matter and are probably Orthic Gleysols.

There are two plant strata : (1) an upper layer of graminoids at 20-25 cm. *Eriophorum polystachion* with its white fruiting heads is the phenological dominant in late summer, though its cover may be lower than that of the associated sedges *Carex paysonii, C. saxatilis, C. bipartita* and *C. eleusinoides*. Total vascular plant cover is ca. 10-15%. *E. polystachion* also grows in pure, dense stands in shallow water of high subalpine ponds. (2) The moss *Calliergon sarmentosum* forms a dark surface layer.

19. *Sphagnum* bog type.

Ponds and communities of the preceding type are bordered by hummocky ground. Hummocks encircling *Eriophorum* communities are species-rich in hepatics (*Leiocolea muelleri, Lophozia* spp., *Barbilophozia hatcheri, Cephalozia, Cephaloziella, Scapania irrigua*) and mosses (*Aulacomnium palustre, Tomenthypnum nitens, Hylocomium splendens, Bryum pseudotriquetrum, Dicranum scoparium, Paraleucobryum enerve, Sphagnum warnstorfii, Polytrichum commune, P. juniperinum*). The hummock tops also have fruticose lichens: *Cladonia pleurota, C. chlorophaea, C. coccifera, C. ecmocyna, C. pyxidata, Cladina mitis, Cetraria ericetorum.*

Timberline ponds are bordered by hummocks mainly of *Sphagnum russowii*. Associated bryophytes include many of the above. There are also some sedges and *Kalmia polifolia*.

20. *Salix barrattiana* scrub type.

This type is represented in the study area by a few small patches at the S end. It is much better developed along high subalpine valleys e.g. Evelyn Creek (Appendix 4). Structurally it entails : (1) a fairly dense layer of 3-5 dm tall *Salix barrattiana*; (2) a variably dense layer of forbs, the same species as in herb meadows; (3) a carpet of bryophytes. Spruce trees have invaded some of the scrub meadows.

21. *Artemisia michauxiana/Rubus idaeus* type.

This type is represented by one small (0.2 ha) stand on a steep, W-facing shale scree slope at 2250 m. The unstable surface has ca. 10% cover of clones of *Artemisia michauxiana* and short (30 cm) *Rubus idaeus*. There are local patches of a few other species, notably *Penstemon ellipticus* which occurred only here.

A. michauxiana is characteristic of cliff ledges on both warm and cool aspects, but here it occupies a different and, for it, rather large expanse.

22. *Populus tremuloides* scrub type.

One small stand of dwarfed aspen was found, at 2000 m on a steep SE-facing slope of loose shale pebbles. The *Populus* vegetation, apparently one clone, formed an open shrub cover less than 1 m tall and interconnected at the

roots. There was no sign of sexual reproduction.

On the bare shale were scattered plants of *Juniperus communis*, *Rosa acicularis*, *Rubus idaeus*, *Shepherdia canadensis*, *Fragaria virginiana*, *Carex brevipes*, *Epilobium latifolium*, *E. angustifolium*, *Aster sibiricus* and *Saxifraga bronchialis*. The shrubs are important constituents of montane and subalpine forests, but at their upper elevational limits here. The S aspect must be the key to their survival. The soil temperature (-15 cm) on 19 Sept 1970 was 7°C here but only 1-2°C over most of the tundra.

The notion must be entertained that this community type, though distinct from subalpine forest and meadow vegetation, is not really a tundra type.

23. *Abies-Picea* krummholz type.

This type occurs at 2100-2250 m, exceptionally to 2350 m, mainly on SE-facing hillsides and E crests of ridges (Plates 4,5). The key factor in its success is snow cover, specifically the narrow range and delicate balance between deficient and excess snow accumulation. Some winter snowcover is essential to protect the conifer branches from windblast and desiccation injury, but deep snow accumulation precludes conifers, probably by not allowing sufficient time for carbohydrate buildup (cf. Billings and Mooney 1968).

Abies lasiocarpa is the major krummholz species, forming prostrate and flagging clumps 0.3-2 m high, taller in the lee of some ridges and plateaux. *Picea engelmannii* is also common, and ranges into more xeric habitats and higher

elevations than *Abies*. On Signal Mt., Hrapko (1970) found *Picea* attaining higher elevations than *Abies* on all slopes. Krummholz *Pinus contorta* is quite rare in the Bald Hills, and *P. albicaulis*, a timberline conifer seen in some of the park ranges, is wanting. Adjacent to some *Abies-Picea* krummholz stands are small dense patches up to 0.5 m tall of *Betula glandulosa*.

Practically all krummholz is associated with *Dryas octopetala*, *Cassiope tetragona*, *Phyllodoce glanduliflora* or *Salix arctica*, on a loose shaly surface. *Vaccinium vitis-idaea* and *Salix nivalis* are also usually present, along with a few forbs and graminoids. The general ground vegetation is, then, most similar to the *D. octopetala*/lichen community type but with the inclusion of species such as *Phyllodoce glanduliflora* in response to snow accumulation around the krummholz clumps. Within larger stands of *Abies* krummholz there are clones of *P. glanduliflora* and *Vaccinium scoparium*, thick clumps of mosses (*Dicranum* spp., *Polytrichum* spp.) and fruticose lichens especially *Cladonia* spp., *Cetraria* spp., *Cladina mitis* and *Stereocaulon alpinum*.

A few conifer individuals penetrate into *Cassiope mertensiana* heaths and even *Carex nigricans* snowbeds, but this is probably a transient phenomenon rather than the beginnings of forest invasion such as reported for timberline meadows in west-coast ranges (Fonda and Bliss 1969, Franklin et al. 1971).

Forest-tundra mosaic

The superposition of trees over a tundra landscape creates complications in the analysis and description of the vegetation. Trees are one to four orders of magnitude larger than tundra plant species. Some conifer clones are larger than entire tundra plant communities, and microclimatic effects are proportionately greater. Clearly, any one unit of vegetation cannot handle treed and treeless tundra on an equivalent basis. That is why, although tree-dotted tundra does contain various tundra community types, this study treats it in a zonal or landscape context, viz. the forest-tundra zone.

The forest-tundra mosaic in the Bald Hills comprises conifer clumps dispersed over a matrix chiefly of heath tundra together with some stony tundra, herb meadow and snow-bed communities. *Abies lasiocarpa*, the most important conifer, forms islands up to 10 or more meters in diameter. The island growth-form comprises a core of up to 20 or more leaders, height 1-4 (exceptionally to 7) m, the tops often conspicuously reddened, ringed by a dense layer of prostrate spreading branches 3-7 dm high. In the forest-tundra stand that was inventoried (Table 19), conifer canopy cover was 16%, of which 94% was *Abies*. There are areas in the forest-tundra zone with greater canopy cover, the *Abies* so thick that one cannot avoid walking over the prostrate branches. But taken as a whole the forest-tundra zone has only 5-10% conifer cover. *Picea engelmannii*, sometimes as numerous but much less important in cover than *Abies*, is never layered and

TABLE 19. Inventory of conifers and associated ground vegetation in a 45x135 m area of the forest-tundra zone.

CONIFER SPECIES	*ABIES LASIOCARPA*	*PICEA ENGELMANNII*	*PINUS CONTORTA*	TOTAL
NO. CLONES	32	34	4	70
MEAN CROWN COVER (m^2)	29.0±4.2[a]	1.6±0.3	1.7	
% RELATIVE COVER	93.8	5.5	0.7	100.0
% GROUND COVER	15.3	0.9	0.1	16.3
MEAN HEIGHT (m)	2.8±0.1	1.6±0.1	0.8	
ASSOCIATED GROUND VEGETATION[b]				
Phyllodoce glanduliflora	30	18	1	49
Cassiope tetragona	3	10	0	13
Vaccinium scoparium	6	5	0	11
Empetrum nigrum	3	7	1	11
Dryas octopetala	1	1	1	3
Salix nivalis	0	1	0	1
Cladonia sp.	1	0	0	1
bare surface	0	1	1	2

[a]Standard error.

[b]Numbers of occurrences of dominant species adjacent to conifer clones.

generally not as tall. *Pinus contorta* is very uncommon. It forms short, straggly specimens often with much dead wood in the upper portion.

Tree clumps in the forest-tundra zone have much more influence on adjacent vegetation than does krummholz, which moderates only its internal microclimate. *Abies* is much more influential than *Picea*. In the study plot, *Picea* was often surrounded by *Cassiope tetragona* and other tundra species requiring little snowcover, whereas *Abies* was in almost all instances surrounded by *Phyllodoce glanduliflora* and *Vaccinium scoparium* (Table 19). The heath cover was densest at the outer edge of the fir apron. Herbs were very scarce except for occasional clones of *Epilobium angustifolium*. *Dicranum* spp., *Barbilophozia hatcheri*, *Ptilidium ciliare*,

Polytrichum spp. and *Cladonia* spp. were abundant within the *Abies* islands especially if these were open-centered (25% were of this configuration in the study plot). Epiphytic growth was very poor, mainly *Parmeliopsis ambigua, P. hyperopta* and *Cetraria pinastri* near the base, and *Lecanora varia* and *Buellia disciformis* on branches.

Phenology of species adjacent to and within *Abies* islands is delayed about 2 weeks compared to their development on open tundra.

TRANSECT STUDIES

Bald Hill transects

Data from two of the transects on the Bald Hill are presented in Tables 20 and 21. The third transect had no discernible patterns and has therefore been excluded.

Dryas octopetala is the outstanding dominant in the short S-N transect (Table 20). *Dryas* cover values of 20-25% signify virtually complete mat cover ("canopy cover"). The remaining vascular plant cover is rather low and species-poor. Cryptogam cover, especially of fruticose lichens, seems correlated with *Dryas* cover. No other clear patterns emerge.

The long E-W transect (Table 21, Appendix 7) brings out several points : (1) Pooling the data into 8-quadrat means still leaves a good deal of "noise". Evidently a considerable number of 25x25 cm quadrats, or a fair number of very large ones, would be required for a good approximation

TABLE 20. Percent cover of plants in a 55 m S-N downslope transect in *Dryas*/lichen tundra on the Bald Hill.

TRANSECT SEGMENT[1]	1	2	3	4	5	6	7	8	9	10	11	12
VASCULARS												
Luzula spicata	2											
Carex sp.		+*										
Pedicularis arctica	2	2			+	2						
Festuca brachyphylla	2						2					
Antennaria alpina	2			1	1	2		+				
Artemisia norvegica	5		+		2	2	2	2				
Campanula lasiocarpa		1		+	+			+				+
Salix nivalis	5	2	7	2	11			2		2		
Dryas octopetala	15	24	20	24	10	5	29	10	19			7
Vaccinium vitis-idaea		2	2	2	+	2	5	2	7	3	2	11
Gentiana glauca				5		+						
Trisetum spicatum					+							
Poa alpina					+	2	2					
Salix arctica						2	5		2			2
Arenaria obtusiloba												+
Cassiope tetragona												2
LICHENS												
crustose	1					+	2	2	1	1	2	2
foliose						+			2	2		
fruticose	15	38	38	15	20	15	39	19	9	2	1	2
ROCKS >6cm diam.								2	8	3	3	8
PEBBLES	39	2	2	1	1	19	8	33	39	74	85	15
MINERAL SOIL	2	2	3	2	2	9	1	2	1	1	3	2
LITTER	3	8	26	38	26	26	26	19	20	2	+	26
SUM VASCULAR COVER	31	29	28	33	24	15	44	15	27	5	2	21
SUM BRYOPHYTE COVER	9	15	3	39	33	9	3	2	3	8		2
SUM LICHEN COVER	16	38	38	15	20	16	41	21	11	4	2	4

[1]Mean of two 25x25 cm quadrats.

*Less than 0.5% cover.

TABLE 21. Percent cover of plants in a 375m E-W transect across *Dryas*/lichen tundra on the Bald Hill.

TRANSECT SEGMENT[1]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
VASCULARS																			
Vaccinium vitis-idaea	7	3	2	2	1	2			2										
Saxifraga ?caespitosa	1	2							+	1	1								
Campanula lasiocarpa	+	+	+	+		+			+	+		+							
Carex nardina	1	1	+	+	+	1	+	1								+			
Carex albonigra	+	1		1	+	+		+								+			+
Dryas octopetala	13	5	14	10	5	4	3	3	7	15	4	3	10	7	6	9	25	12	22
Salix nivalis			2	1	1	3	2	1	1	1	1	3	+	+	2	11	5	3	4
Potentilla nivea				+	1		1												
?Trisetum spicatum					+	+	+												
Antennaria alpina		1	+	2	1		+	+	1	+						1	1	+	1
Draba sp.			+													+		+	
Luzula spicata				1	+				+	+				+		1	+	1	1
Silene acaulis				+		+					+								+
Poa alpina										+									
Arenaria obtusiloba						+				+		+	+		+	1	2	1	+
Festuca brachyphylla									+	+	+	1				1	1	3	1
Polygonum viviparum									+	+			+	+			1		+
Pedicularis arctica									+	2						1	1		+
Artemisia norvegica									+							+	2	1	1
Salix arctica										+						2		+	2
Gentiana glauca																+	2	+	1
Cassiope tetragona																	+		
Carex sp.																	1		
LICHENS																			
crustose	2	14	3	12	6	2	2	2	2	1	1	1	1	1	1	19	8	6	1
fruticose	10	16	6	5	3	5	10	8	22	10	3	2	6	5	5	9	13	7	13
foliose	11	21	12	8	7	7	4	1	+	1	4	1	+	1	1	+	2	+	1
CONGLOM. PEBBLES	34	47	17	32	37	20	8	9	1	1	3	1	2	2	2		+	1	
SHALE PEBBLES	12	16	47	35	47	52	72	66	45	34	85	79	62	73	63	5	2	30	36
MINERAL SOIL	1	1	1	3	+	1	1	+	4	1	+	+	1	1	1	1	4	19	5
LITTER	14	6	23	18	14	17	8	10	29	37	4	10	17	13	15	59	63	25	37
SUM VASCULAR COVER	20	13	18	16	8	10	6	6	13	20	7	6	11	8	9	26	41	22	32
SUM BRYOPHYTE COVER	+	1	1	5	1	4	1	1	16	4	2	2	2	1	2	18	3	5	7
SUM LICHEN COVER	23	50	21	25	16	14	16	11	24	12	8	3	7	6	6	27	23	14	15
NO. VASCULAR SPECIES	4	4	4	6	3	5	3	2	4	5	2	2	2	2	2	8	10	8	7

[1]Mean of 4 pairs of 25x25 cm quadrats, each pair at 5 m intervals.

NOTE: Transect segment 1-4: Gentle E-facing slope, conglomerate bedrock surface; thin winter snowpack.

5-9: W-facing slope, conglomerate bedrock surface; snowfree ± all year.

10-15: Level ridge, shale-pebble surface; up to 30 cm snowpack.

16-19: Gentle E-facing slope, shale & conglomerate; up to 80 cm snowpack.

of the plant cover.

(2) From conglomerate to shale there are no real differences in *Dryas octopetala* or *Salix nivalis* cover. *Carex nardina, C. albonigra* and *Vaccinium vitis-idaea,* on the other hand, are apparently restricted to the more stable conglomerate surface. The variety of species that can occur on this substrate (cf. Table 15, stand 7) was not realized, possibly due to the extreme exposure.

(3) Vascular plant cover and species richness rise markedly at the mesic W end of the transect (Table 21). Plants such as *Gentiana glauca, Artemisia norvegica* and *Salix arctica* evidently prefer the less windy, less xeric habitat, even if it means competing with *Dryas octopetala* which forms almost total mat cover. A number of vascular plant species drop out at the W end, presumably due to competitive pressure. There is also a shift away from saxicolous lichens to mesophytic species such as *Stereocaulon alpinum* and *Lepraria neglecta* (Appendix 7).

(4) The cover of saxicolous lichens, both crustose and foliose (mostly *Umbilicaria*) types, is highest at the E end of the transect. Their poor development over the remainder may be due to wind abrasion (segment 5-9), surface instability (segment 10-15), and overtopping by vascular plants (segment 16-19).

(5) Cryptogam cover (aside from saxicolous lichens) is more or less correlated with *Dryas* shoot cover and with litter which is mostly dead *Dryas* leaves. In

some *D. octopetala*/lichen communities the bryophytes, most fruticose lichens and many crustose species are wholly dependent on *Dryas* as substrate (cf. Chapter 7).

(6) Quadrat segments 9-10 form a definite vegetational discontinuity. The concave and presumably more sheltered surface may have enhanced the success of vascular plants and cryptogams.

Snowbed meadow transect

This transect (Table 22) traverses two communities, a snowbed (quadrats 1-9, =stand 17) dominated by *Luetkea pectinata* and *Carex nigricans*, and a herb meadow (=stand 20), nearest the *Artemisia norvegica-Luzula parviflora* community type (Appendix 5). Quadrats 10-11 form a hiatus, most obvious in lichen cover and variety.

There is a slight upslope gradient of decreasing winter snowcover and soil moisture. Shifts in species composition and cover along the transect are moderate. About half the vascular and lichen species occur over most of it. Total plant cover and numbers of species are comparable throughout. Important discriminatory species are *Luetkea pectinata*, occupying only the hydric end, and *Salix arctica*, absent from this end. Lichens are poorly represented at the hydric end. A few species of bryophytes occur at only one or other end. In quadrats 10 and 11 *Drepanocladus uncinatus* has a high cover, *Lophozia* spp. are entirely absent, and lichen cover is very low.

Although in the field there seemed to be four distinct

TABLE 22. Cover estimates[1] of all plants in 2x5 dm quadrats in an upslope transect of snowbed meadows.

QUADRAT NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
VASCULAR PLANTS																				
Ranunculus eschscholtzii	+	+																		
Epilobium alpinum	+	+	+																	
Luetkea pectinata	4	1	1	3	3	3	4	3	1											
Antennaria alpina	+			+	+	+	+	+	+											
Carex nigricans & C. pyrenaica	4	2	3	+	+	1	+	1	2	1	2	1	1	+	+	+				
Erigeron peregrinus	+	1	1	1	+	1	+			+	+	1	+	+	1	+	+		+	
Juncus drummondii	+			+	+	+	+	+	+	+		+		+	+	+	+	+	+	+
Sibbaldia procumbens	+	+	+	+	+	1	+	+	3	1	2	2	2	2	1	2	1	+	1	+
Veronica wormskjoldii	+	+	+	+	+	+	+			+	1	+	+				+		+	+
Antennaria lanata	+	+	1	1	+	+	2	1	+	1	+	1	1	1	1	2	2	1	1	1
Artemisia norvegica		+	+			+						+						1	1	+
Caltha leptosepala			1																	
Polygonum viviparum					+															
Deschampsia atropurpurea			+	+	+			+	+	+	1	1	+	1	+	+	+	+		
Carex spectabilis				+	+							+			+	1	+	1	1	+
Gentiana glauca					+				+				+		+					
Salix arctica					+	1	1	2	+	4	2	2	1	2	1	2	2	2	2	2
Phyllodoce glanduliflora						+											1			
Luzula parviflora										1	1									
Festuca brachyphylla												+								
Phleum alpinum												+						+		
Hieracium gracile												1		+		+	+	+	1	
Castilleja occidentalis												1	+	+		+		+	+	+
Potentilla diversifolia																	+	+		
Arenaria obtusiloba																		+		
Luzula spicata																			+	
Agrostis variabilis																				+
Poa cusickii																				+
BRYOPHYTES																				
Aulacomnium palustre	+	2																		
Polytrichastrum alpinum	1	+	+																	
Rhacomitrium sp.	+							2												
Brachythecium salebrosum	+		+				+			2										
Drepanocladus uncinatus	3	3	4	3	+		+		2	4	5	1	+		+					
Lophozia spp. & *Barbilophozia hatcheri*	3	3	1	2	+	+	1	2	2			2	2	2	+	+	1			+
Dicranum scoparium & *Kiaeria starkei*	+		+	2	4	4	3	+	2	1	1	1	4	1	3	3	1	+	3	1
Paraleucobryum enerve			+		+															
Conostomum tetragonum					+															
Ditrichum flexicaule							+		+											
Polytrichum commune								+	+	+	+	+	+	+	+	+	+	+	+	+
Bryum sp.												+								
Polytrichum piliferum																1	3	1		1
LICHENS																				
Cladonia ecmocyna	+	+			+	+	+	1	+		+	+	1	1	1	+	1	1	1	1
Peltigera rufescens	+		1	1	1	1	1	1	1	+	+	+		1	1		+	4	1	2
Stereocaulon alpinum	+			+	+	+	+	1	2		+	+	1	+	+	+	+	+	1	1
Cladina mitis	+			+	1	1	+	+				1	2	1	1	1	1	+	1	1
Cetraria ericetorum & *C. islandica*			+	1	+			+	+			1		+		+	+	+	1	+
Cladonia coccifera & *C. pyxidata*				+	+	+		1	1			+	+	1	1	+	+	+		
Ochrolechia geminipara					1	+			+											
Psoroma hypnorum					+												+			
Solorina crocea						1														+
Cladonia decorticata							+	1	1											
Arthrorhaphis citrinella									+											
Lepraria neglecta													+	+	1	1	+	+		
Buellia papillata														+		+				
Lecidea granulosa															+					
PEBBLES		+		+																
LITTER	4	4	4	3	4	3	3	3	4	3	2	4	4	4	4	4	4	3	3	4
VASCULAR PLANT COVER	4	3	4	4	4	4	4	4	4	5	5	4	3	4	3	4	4	4	4	3
BRYOPHYTE COVER	4	5	4	4	4	4	3	4	4	5	5	3	4	3	3	3	4	2	3	3
LICHEN COVER	+	+	1	2	2	3	1	2	3	+	1	1	3	3	3	2	2	4	2	3
SUM VASCULAR SPECIES	10	9	10	10	13	11	9	8	9	9	8	14	9	9	9	10	11	12	11	10
SUM BRYOPHYTE SPECIES	7	4	6	3	5	2	5	4	5	4	3	5	4	3	4	4	4	3	2	4
SUM LICHEN SPECIES	4	1	2	5	8	7	5	7	8	1	3	6	5	8	7	7	8	7	5	6
SUM ALL SPECIES	21	14	18	18	26	20	19	19	22	14	14	25	18	20	20	21	23	22	18	20

[1]Cover scale: +<1% cover, 1=1-5%, 2=6-15%, 3=16-25%, 4=26-50%, 5=51-75%, 6=76-95%, 7=ca.100%.

communities, one would be hard-pressed to pick them out of the transect data. This underlines the important role that some species play in our visual impression of communities. *Antennaria lanata* is particularly significant. It may not have a high cover but its strikingly pale color stands out against the overall dark background, hence small shifts in its percent cover result in large changes in the community's appearance. Color, height and other properties of associated plant species are also significant in enhancing or muting the effect. *Luzula parviflora* is another species whose aspectual dominance is striking; in quadrats 10 and 11 (Table 22) it was much more conspicuous than any other species.

Dryas/lichen to *Carex nigricans* transect

This transect (Table 23, Appendix 6) yielded the most valuable information. It encompasses three major noda : (1) pebbly tundra with poor soil development, low bryophyte and vascular plant cover, and high lichen diversity; (2) snowbed with a depauperate flora dominated by *Carex nigricans*; (3) all vegetation between these endpoints, and dominated by heath species. The community sequence is indicated in Fig. 16.

Major trends seen in the transect are these :

(1) Pebble cover is very high in the first 23 quadrats but decreases abruptly at the start of heath vegetation. Litter accretion and soil development are much more significant processes in heath vegetation than on *Dryas*-

TABLE 23. Cover estimates of selected plant species in a transect from *Dryas octopetala*/lichen tundra to *Carex nigricans* snowbed.

TRANSECT SEGMENT[a]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Lecidea sp.	+[b]	+	+																				
Hypogymnia intestiniformis	+	+	8																				
Cetraria commixta	+	1	5	1	+																		
Lecanora polytropa	+	+	+	+	+	+																	
Cetraria tilesii		+	+	+	+																		
Alectoria nigricans & A. ochroleuca		+	+	+	1																		
Rhizocarpon cf. geographicum	+	+	+	+	+	+		1															
Thamnolia subuliformis	+	+	+	+	+	+	+	+															
Rhacomitrium lanuginosum	+		1	+	+	+	+	+	+														
Cetraria cucullata & C. nivalis	+	+	+	+	+	1	3	2	1														
DRYAS OCTOPETALA	5	3	1	4	2	3	5	4	9	+													
VACCINIUM VITIS-IDAEA		+	1	11	2	+	+	+	+	+													
SALIX NIVALIS	+	1	1			1	+	4	2	4	1												
Dactylina arctica			1	+			+	+	2	+													
CAMPANULA LASIOCARPA		+				+	+	+	+	+	+	+	+										
Polytrichum piliferum	+	1	2	2	1	1	+	1	2	2	+	+	+	+	+	+	+						
Stereocaulon alpinum	+	+	+	1	2	9	4	1	1	+	1	+	1	+	+	+		+	+	+			
Cladina mitis	1	1	+	4	2	+	2	2	5	2	4	3	2	1	1			+		+			
Dicranum scoparium	+	+		+	1	1	2	5	9	7	8	4	5	4	4	1	4	+	1	+			
Cetraria ericetorum & C. islandica	+	+	+	+	+	+	1	1	2	2	+	+	2	+	+	1	2	1	1	+			
Bryum spp. & Pohlia cruda			+	+	+		+	+		+	+	+	1	+	+	+	+		1				
Cladonia ecmocyna		+	+	2	2	+	2	4	2	3	4	2	1	+	2	1	1	1	+	+	+		
Cladonia coccifera		+	1	4	1	+	2	1	2	2	4	+	1	+	+	+	+	+	+	+	+	+	
Lophozia s.l.[c]	+		+		+	+	+	+	+	+	3	1	3	3	4	2	4	4	2	5	2	1	
Ochrolechia cf. geminipara							7	+	+														
CASSIOPE TETRAGONA							13	28	16	8	3	3											
ARTEMISIA NORVEGICA							+	+	1	+	+	+	+										
GENTIANA GLAUCA							+	+	+	+	+	+	+										
SALIX ARCTICA							+	+	2	1	2	1	+	1	1								
Conostomum tetragonum							+		1	1	+	+	+	+	+								
Peltigera aphthosa							1	1	1			+	3		2	4		+					
Gymnomitrium concinnatum & Anthelia juratzkana							1	1	+	+	3	4	2	4	2	+	3		1				
Lepraria neglecta								1	2	7	2	4	2	1	3		1	+	4	1	1		
PHYLLODOCE GLANDULIFLORA									4	7	18	26	20	+		+	3	8	+	10	1		
SIBBALDIA PROCUMBENS									+	+	+	1	1	+	+	+	+	+	+		+		
CAREX NIGRICANS & C. PYRENAICA									+	2	+	+	1	+	+	2	2	3	3	13	4	68	72
CASTILLEJA OCCIDENTALIS											+	+	+										
ANTENNARIA LANATA										+	+	+	+	+	+	2	3	2	3	2	8	+	
Polytrichastrum alpinum/lyallii										+	+	+	+	+	+	+	+	+	+	+	+	+	+
CASSIOPE MERTENSIANA													11	38	38	25	6	1					
Solorina crocea												+	+		+	+	6	+	+	2	1	1	
Drepanocladus uncinatus													+	1	+	1	+	+	+	+	+	+	+
DESCHAMPSIA ATROPURPUREA													+	+	+	+	+	+	+	+	2	2	2
LUZULA PARVIFLORA														+	+	+	1	+	1	1			
Kiaeria starkei														+	7	14	4	18	15	15	15	6	
JUNCUS DRUMMONDII																+	+	+	+	+	+		
LUETKEA PECTINATA																5	19	17	22	8	33	4	
PEBBLES	74	90	69	29	48	75	3	8		+	+							+					
MINERAL SOIL	1	+			+	+	4	22	1	2	6	+	1		1				1				
LITTER	16	10	5	10	8	5	33	29	38	39	33	56	39	38	56	38	29	39	38	38	29	24	26
VASCULAR PLANT COVER	5	4	3	11	4	3	18	30	38	24	29	38	38	44	38	38	38	35	35	38	56	74	70
BRYOPHYTE COVER	1	2	2	3	2	1	5	6	13	10	13	7	18	15	19	18	15	22	24	19	18	16	2
LICHEN COVER	1	4	17	13	8	10	20	13	18	18	15	10	18	3	7	8	8	3	7	5	3	1	
SUM VASCULAR SPECIES[d]	2	4	3	2	2	4	8	8	11	12	11	10	11	9	7	9	9	9	8	7	7	4	2
SUM BRYOPHYTE SPECIES	3	1	3	2	3	3	5	4	5	5	5	5	6	6	7	6	6	4	5	4	4	4	2
SUM LICHEN SPECIES	10	15	15	14	13	10	11	13	11	8	7	9	9	7	9	7	6	9	7	8	4	2	0
SUM ALL SPECIES	15	20	21	18	18	17	24	25	27	25	23	24	26	22	23	22	21	22	20	19	15	10	4

NOTE: Vascular plant species in CAPITALS, bryophytes in Lower-case, lichens in *Italics*.

[a]Mean of four 2x5 dm quadrats at 5 dm intervals.

[b]Less than 0.5% cover.

[c]Includes Barbilophozia hatcheri and Lophozia spp.

[d]Includes all recorded species, as 4-quadrat means.

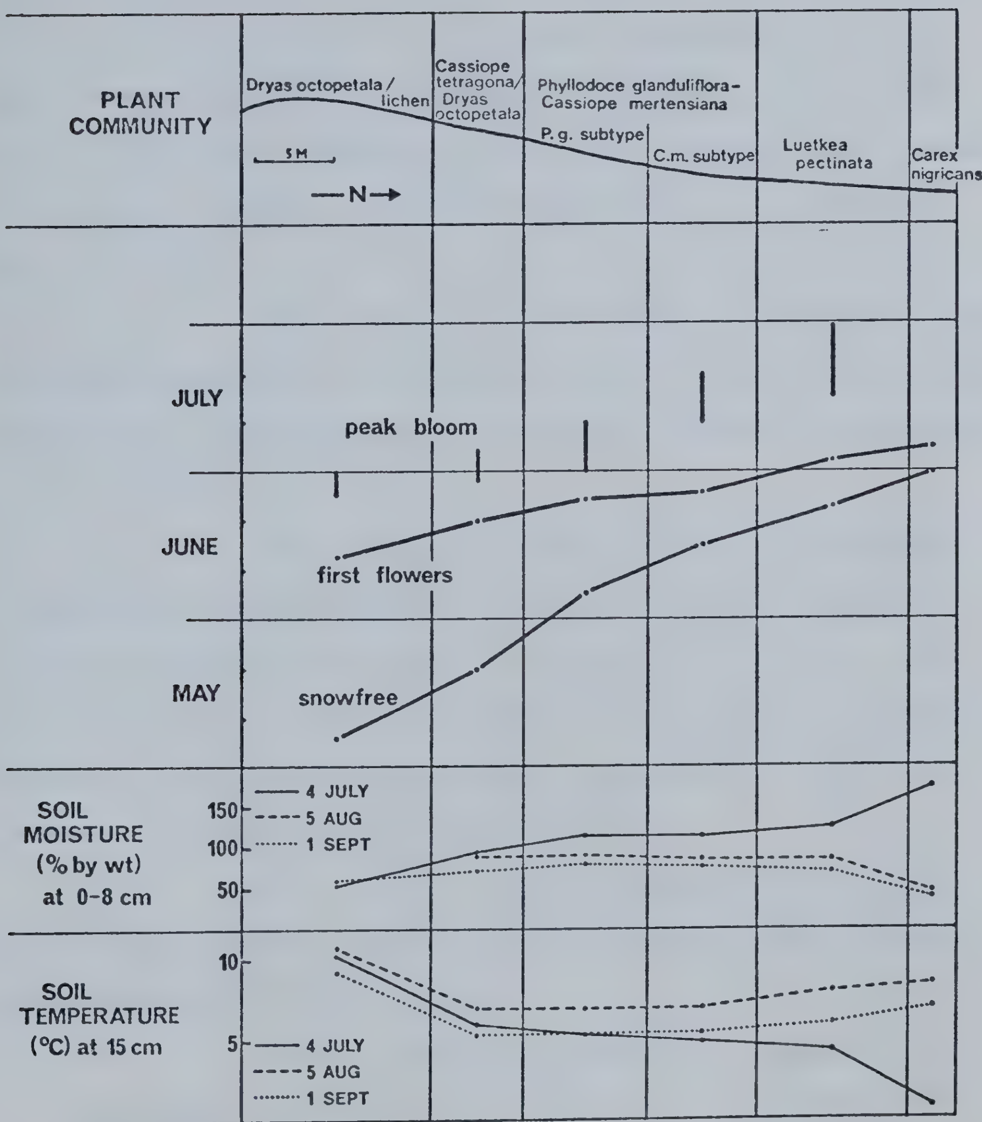


FIG. 16. Soil moisture, soil temperature, and phenological events across the *Dryas*/lichen to *Carex nigricans* transect.

dominated surfaces.

(2) Mineral soil is exposed mainly in the *Cassiope tetragona/D. octopetala* community. Cover of organic matter in this most xeric of the heath communities is not quite enough to exclude needle-ice formation. There seems to be a correlation between mineral soil surface and presence of a few plant species especially *Salix nivalis* (also cf. Figs. 13 & 14).

(3) Vascular plant cover is lowest and most heterogeneous in the *Dryas*/lichen segment. It is remarkably homogeneous in the *Cassiope mertensiana* segment, and highest in the snowbed.

(4) Bryophyte cover is low and irregular in the *Dryas*/lichen segment. Through the heath sequence it is not as uniform nor as high as vascular plant cover, and it declines in the snowbed. Dominant bryophytes are *Dicranum scoparium* in the xero-mesic heaths, and *Kiaeria starkei* and *Lophozia* s.l. in the hydro-mesic heaths.

(5) Lichen cover is highest in the first half of the transect, and nil in the snowbed. The lichens can be assigned to four groups :

i. Saxicolous species, restricted to the first third of the transect and accounting for most of its species richness.

ii. Species on soil and litter in relatively unshaded microhabitats. These species, notably fruticose forms such as *Cetraria nivalis*, *C. cucullata*,

Dactylina arctica and *Alectoria* spp. occur in only ca. the first 40 quadrats, i.e. the same range as *Dryas octopetala*.

iii. A few species across most of the heath segment, with *Solorina crocea, Lepraria neglecta* and *Peltigera aphthosa* the most important.

iv. A relatively large group of fruticose species of wide ecological amplitude, important ones being *Cladonia ecmocyna, C. coccifera, Cladina mitis, Cetraria islandica, C. ericetorum* and *Stereocaulon alpinum*.

(6) The sharpest breaks in overall pattern are at the start of the *Cassiope tetragona/Dryas octopetala* community and at the start of the *Carex nigricans* snowbed. These breaks reaffirm my classification of the Bald Hills vegetation, viz. Stony Tundra, Heath Tundra and Snowbeds, with Herb Meadows off the tundra sequence.

The community sequence is related to snowmelt dates (Fig. 16), which are in turn related to (1) degree of winter snow accumulation and (2) spring weather. Snow accretion is minimal in the *Dryas*/lichen community, increases progressively through the heath sequence, and is greatest in the snowbed community. Meltout always proceeds sequentially from *Dryas*/lichen to snowbed, in a total timespan of ca. 2 months. Snowmelt depends on solar radiation and air temperature, hence rate of retreat of the snowline is not constant from year to year.

Observations on snow accumulation and meltout in other communities (Table 24) amplify the transect data. Most *Dryas*-dominated sites have sparse snowcover and are snowfree by early May. Cushion-rosette communities have variable snowpack, from none to 1 m or more. *Cassiope tetragona/D. octopetala* communities display a remarkable range in snow-depths, from only 15-20 cm in some, exposing the tops of the *C. tetragona* stems much of the winter, to well over a meter (Table 24). Obviously snowdepth, although it may help explain the pattern of plant communities in the Bald Hills, is not the only factor.

Phyllodoce glanduliflora-Cassiope mertensiana communities have more than a meter, to 3+ m of snowpack. Snowbed communities also have deep snowpack. The herb meadow communities that were investigated had very uniform snowcover of 1-2 m. Snowdepth measurements in an *Artemisia norvegica/Salix arctica* meadow and an adjacent slightly drier phase revealed a consistent 15 cm difference through the winter. Even though a good correlation may be demonstrated between herb-meadow community patterns and snowdepth, it is not considered to be the governing factor.

PHENOLOGY

General patterns

In the Bald Hills the growing season for vascular plants extends from early May to late August. Fall coloration is normally conspicuous by the last week of August.

TABLE 24. Snowdepth (cm) at various plant communities in the Bald Hills through the winter of 1970-71, based on 2-6 measurements per site per date.

ELEVATION	ASPECT & DEG. SLOPE	SITE & COMMUNITY	1970				1971					
			13 Sept	16 Oct	11 Nov	16 Dec	27 Feb	26 Apr	9 May	27 May	5 June	21 June
2300	0	*Dryas*/lichen: top of the Bald Hill	-	0-3	0-2	3-4	0-1	0	0	0	0	0
2300	0	*Dryas*/lichen: saddle area of the Bald Hill	-	0-10	1-20	25-35	30-60	45-80	-	0	0	0
2250	N3	*Dryas*/lichen[1] (Stand 3)	4-15	5-15	5-10	-	25-55	30-40	10-20	0	0	0
2285	S5	*Artemisia norvegica/Dryas*	-	-	-	25-45	60-80	40-60	60	20	0	0
2140	0	*Dryas/Polytrichum piliferum*	5	7-11	-	30-40	55-60	50-60	30-35	0	0	0
2200	NE7	*Cassiope tetragona/Dryas*[2]	-	5-15	5-10	15-30	90?	-	-	0-5	0	0
2240	E10	*Cassiope tetragona/Dryas*	6	-	15	50	110-140	135	105	60-80	25	0
2140	N3	*Artemisia norvegica/ Salix arctica*	5-9	-	17-22	50-55	90	95	70	0-20	0	0
2225	0	*Artemisia norvegica/ Luzula parviflora*	5	-	20-30	60-70	110-130	95-135	85-90	45-55	0	0
2200	NE7	*Cassiope mertensiana - Phyllodoce glanduliflora*	-	20-30	-	15-30	50-75	180	100-120	-	-	-
2130	E	forest-tundra zone overall	-	15-20	30	60-75	90-160	110-155	-	50-85	-	-

[1]Tops of terracettes were snowfree all winter.

[2]Some *Cassiope tetragona/Dryas* communities appeared to have only 15-30 cm snow all winter.

A few plants e.g. *Arabis lyallii* and *Arenaria obtusiloba* may show re-initiation of growth and a second flowering in early September.

Earliest to flower and shed seed are plants on warm aspects with little snow cover, e.g. those of the *Ranunculus gelidus-Erysimum pallasii* (Fig. 17) and *Kobresia bellardii* communities. Next are *Dryas*-dominated communities : dormancy in some species is broken by early May and the overall flowering peak is late June - early July (Figs. 17,18). The peak in heath communities is early to mid-July (Figs. 17,19), and in snowbed communities mid- to late July (Fig. 17). Snowbed grasses e.g. *Deschampsia atropurpurea, Phleum alpinum* and *Trisetum spicatum* are the latest-flowering of all Bald Hills plants that manage to shed seed. *Phleum alpinum* can be in anthesis in the first week of August yet shedding seed by mid-September (Fig. 15). Some species in snowbeds never can complete the cycle, and population replacement must come from without the community.

The phenological sequence can be correlated with snow release dates (Fig. 16). From early-release through to snowbed communities there is a progressively shorter period between snow disappearance and flowering; i.e. early-release communities effectively delay flowering while late ones flower very soon after meltout. A common phenomenon in both arctic and alpine tundra, according to Billings and Mooney (1968), is the telescoping of phenological events in plants released from snowcover relatively late in the summer. In

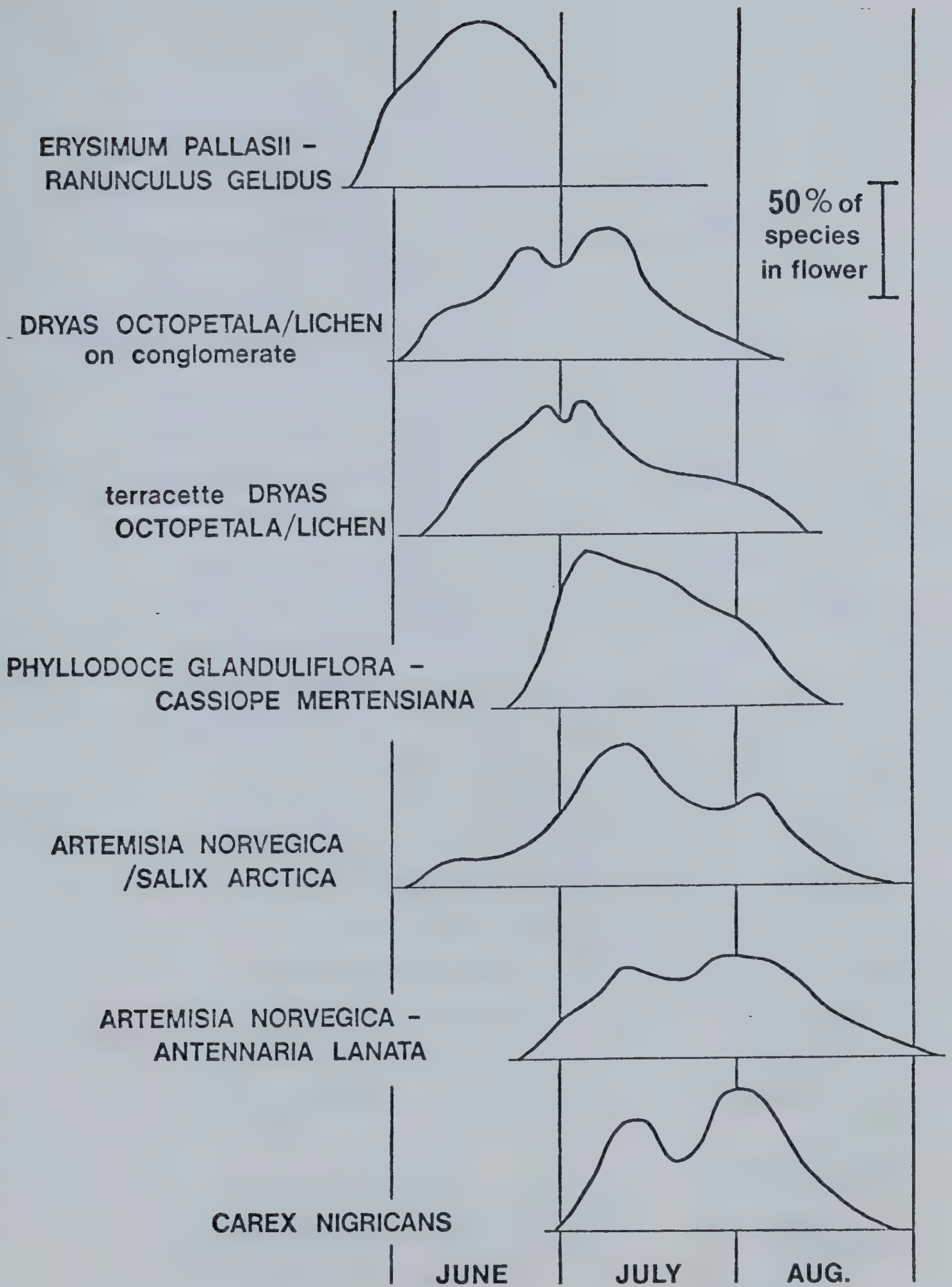


FIG. 17. Phenological curves of seven plant communities in the Bald Hills, 1970.

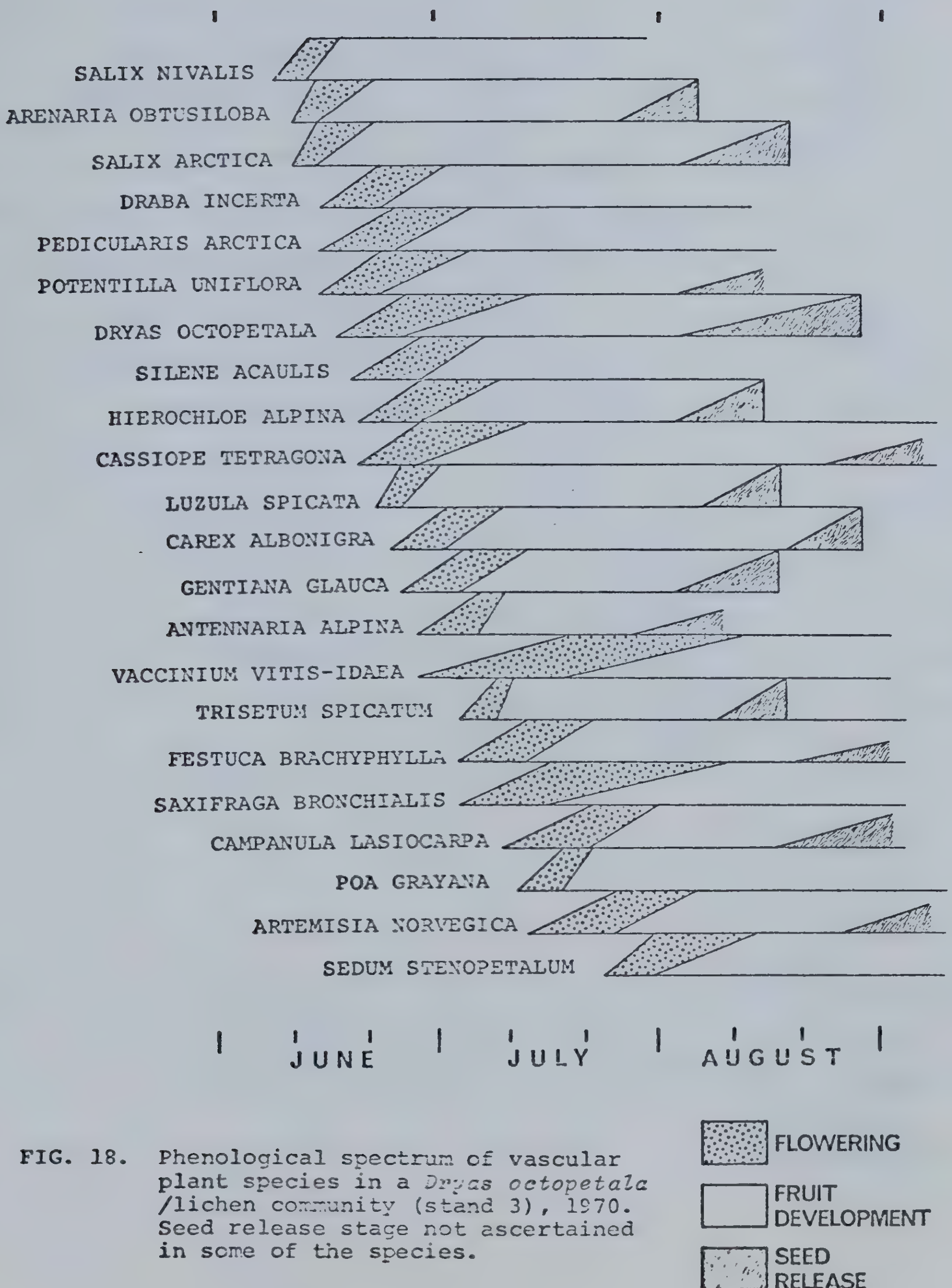


FIG. 18. Phenological spectrum of vascular plant species in a *Dryas octopetala* /lichen community (stand 3), 1970. Seed release stage not ascertained in some of the species.

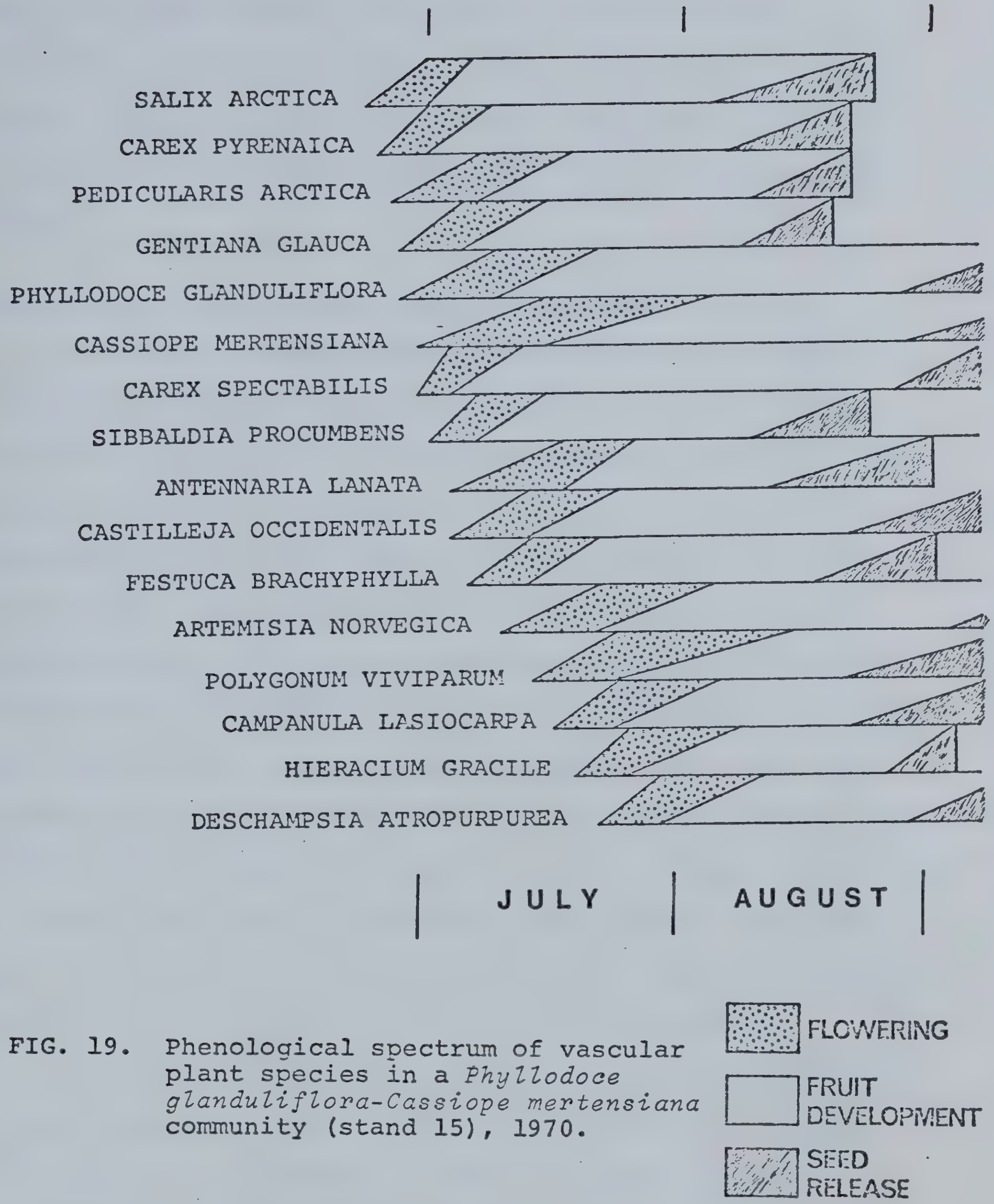


FIG. 19. Phenological spectrum of vascular plant species in a *Phyllodoce glanduliflora-Cassiope mertensiana* community (stand 15), 1970.

the later snow-release communities, plant development is strictly a function of snowmelt (and snowmelt dependent processes such as soil heating) rather than second-order environmental factors such as slope and exposure (Holway and Ward 1965).

Duration of flowering and fruit development

Most of the study area's tundra communities have flowering periods of comparable length (Fig. 17). Their relative briefness circumvents late-season drought or early-season snowcover. Herb meadow communities, on the other hand, enjoy up to three snow-free months with adequate soil moisture. The vascular plant species exhibit a longer phenological sequence (Fig. 15) which optimizes effectiveness of insect pollinators (Mosquin 1971, Pojar 1974). *Senecio triangularis* and *Arnica mollis*, much visited by insects, are very late flowering and support Mosquin's (1971) hypothesis that cornucopian species force the flowering peaks of poorer competitors to occur either later of (in this case) earlier than their own. Herb meadows are unlike most tundra communities where, according to Bliss (1971), flowering is synchronous.

The duration of fruit development appears comparable between community types of dissimilar habitat and species composition. It averages 46 (30-65) days for species in *Dryas octopetala*/lichen tundra (stand 3), 46 (37-63) days in *Phyllodoce glanduliflora-Cassiope mertensiana* tundra (stand 15), and 43 (30-59) days in *Artemisia norvegica/Salix arctica* meadow (stand 21).

Swiftest development is seen in some of the grasses and Compositae, with only 4-5 weeks between onset of flowering and onset of seed dispersal. A minimum of 30 days was recorded for *Antennaria alpina* and *Arnica mollis*. Holway and Ward (1965) found that *Erigeron pinnatisectus* and *Polygonum viviparum* frequently took only a week in alpine tundra in Colorado. In Siberia, Gavriliuk (1961) found the shortest fruiting period in species with small dry seeds, in families such as the Caryophyllaceae, Gentianaceae, some Cruciferae.

Maximum duration of fruit development, ca. 9 weeks, occurs in the heaths (Figs. 18,19). Of vascular plants in Siberian tundra, *Cassiope tetragona* is among the slowest (72 days) in fruit development (Gavriliuk 1961). In the Bald Hills, seed dispersal is more or less synchronous in *Cassiope tetragona, C. mertensiana* and *Phyllodoce glanduliflora*.

<u>The bearing of site on phenology</u>

For most vascular plant species in the Bald Hills, onset of growth is a function of site. Clones of heaths on warm aspects or beside boulders commence flowering up to 2-3 weeks earlier than those in "nodal" heath communities. Flowering is remarkably synchronous between heath communities of a given type, irrespective of slope, aspect or elevation. The most plausible explanation for this is probably synchronous rise in soil temperature.

Some species e.g. *Carex nigricans* and *Veronica wormskjoldii* range from heath through to snowbed sites. Their

seasonal growth may begin up to a month later in snowbeds than in adjacent mesic sites. Species found both in herb meadows and upland tundra communities seem to flower later in the latter. *Artemisia norvegica* blooms synchronously in mesic and xeric sites.

In many species, fruit ripening takes about the same length of time irrespective of site. In others, development in the more mesic sites takes somewhat longer. *Dryas octopetala* in relatively mesic sites (e.g. *Cassiope tetragona/ D. octopetala* communities) begins to flower earlier but takes up to two weeks longer to start shedding fruit (58 vs. 42 days) than in more xeric sites. Holway and Ward (1965) found that fruit development in *Androsace septentrionalis* took from as little as 3 to as much as 9 weeks.

Phenology and elevation

From lowest to highest alpine elevations in the Bald Hills, a range of almost 500 m, the delay in flowering is in the order of a few days. The distribution and depth of snow and the rate of snowmelt, rather than temperature *per se*, are the critical factors in spring. In late summer however, all sites are snowfree and temperature, or more specifically heat units, have a direct bearing on phenology. For example, *Campanula lasiocarpa* required 8-10 days more to ripen fruit in communities at 2250-2315 m than in comparable sites at 2135 m.

By late August - early September, the growing season is definitely past at altitudes above ca. 2400 m. Autumn

coloration is pronounced, the ground surface is frozen, and fresh snow does not melt but accumulates in hollows. At lower alpine elevations at the same time, autumn coloration is prominent but the ground surface is not yet frozen. Arthropod activity is virtually nil. In the forest-tundra zone autumn coloration is just beginning, the ground surface is not frozen and there is still some overt insect activity. In the middle subalpine zone most of the vegetation is still green.

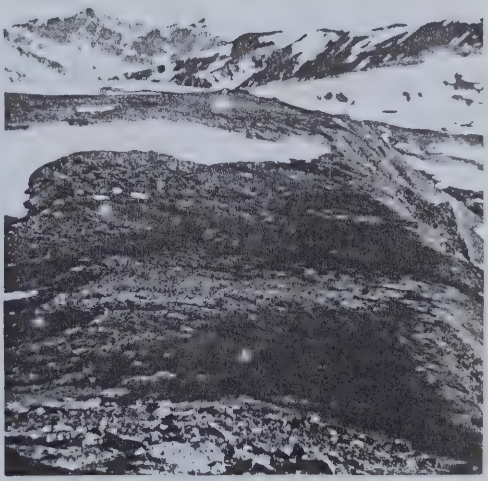
Year-to-year variations

The less snow that a community accumulates the less affected will it be by year-to-year climatic fluctuations. Thus, plants of windy warm slopes flower at about the same time each year, whereas snowbed meadows experience oscillations of a month or more in onset of growth. For example, in 1968 *Luzula* snowbed communities were just beginning to melt out around 25 July, whereas in 1969 and 1970 the same stage had been reached by 12 June (Plate 14), a difference of 6 weeks. By contrast, the difference was only 2 weeks in *Dryas* communities, and the maximum leeway between years in *Phyllodoce glanduliflora-Cassiope mertensiana* communities is ca. 4 weeks. Annual variations in peak flowering of up to two weeks have been reported by Hocking (1968) for *Dryas integrifolia* in the High Arctic.

Phenological development in 1970 was variably delayed relative to 1969. The average and range of delay for selected community types and habitats was as follows :

PLATE 14. Main Station area of the Bald Hills, looking south. Approximately the same stage in snowmelt is seen in both views, but was attained six weeks earlier in 1969 than in 1968.

25 JULY 1968



12 JUNE 1969

S & W-facing slopes	4(-5 to 20) days; <7 days in most species
Earliest *Dryas octopetala* flowers in a range of communities	3(1 to 6) days
D. octopetala/lichen and *Cassiope tetragona/D. octopetala* flowering peak	8(2 to 14) days
Phyllodoce glanduliflora -*Cassiope mertensiana* flowering peak	ca. 15 days

Note that delay is progressively greater in later-release communities. In an alpine area in Banff Park, Beder (1967) found flowering in some species delayed up to a month in 1966 compared to 1965.

Forb meadows contain some species whose phenology is essentially independent of year-to-year environmental fluctuations, and others that show great annual variation (Table 25). Members of the second group are apparently affected more by the growing season than by snow patterns. In some years peak flowering in herb meadows can be delayed

TABLE 25. Dates of appearance of first flowers of certain species in the Bald Hills.

SPECIES	1969	1970	1971	1972
Ranunculus gelidus	24/5	28/5		
Eriogonum androsaceum	14/6	1/7		
Phyllodoce glanduliflora	5/6	5/6	3/6	7/6
Trollius laxus	5/6	6/6	3/6	6/6
Caltha leptosepala	8/6	8/6	5/6	8/6
Ranunculus eschscholtzii	8/6	6/6	6/6	
Senecio pauciflorus	20/6	4/7		24/7
Veronica wormskjoldii	20/6	2/7		23/7
Pedicularis groenlandica	19/6	9/7		25/7

a month relative to other years. According to Holway and Ward (1965), the previous season's environmental conditions may be the critical factor because they influence late-season development of floral primordia. In the Bald Hills, the very dry and warm summer of 1967 was followed by a very poor year of flower production in forb meadows. The damp 1968 and 1969 seasons were followed by seasons of profuse flowering.

GEOGRAPHIC CONSIDERATIONS

Floristic affinities

The Bald Hills contain about half of the vascular plant species occurring in the Maligne area (Kuchar 1972). Absent from the study area are some species in the Opal Hills NE of Maligne Lake, viz. *Aconitum delphinifolium*, *Delphinium glaucum*, *Dryas integrifolia*, *Equisetum scirpoides*, *Papaver freedmanianum*, *Polemonium pulcherrimum*, *Rumex acetosa*, *Salix farriae*, *S. stolonifera*, and *Saxifraga tricuspidata*. Some of these can be related to calcareous substrata, totally lacking in the Bald Hills.

At the N end of the Maligne Range Hrapko (1970) found *Arctagrostis arundinacea*, *Campanula uniflora*, *Festuca baffinensis*, *Pedicularis capitata*, *P. lanata*, *P. oederi*, *Pyrola grandiflora* and about a dozen more species that I did not see in the Bald Hills. Of the 157 vascular plant species that she recorded in alpine tundra on Signal Mountain, Hrapko (1970) considered ca. 30% to have a Cordilleran distribution

and 45% arctic-alpine.

The Bald Hills contain ca. 65% of the above-timberline vascular plant flora of the Alberta Rockies excluding the Waterton-Crowsnest area which belongs to a different floristic region (Kuchar 1973). Only three vascular endemics are known from the Alberta Rockies (Packer 1971), none of these from the Maligne area. The flora is not particularly impressive compared to that in many other mountain areas in the world, where 10-20% endemism and a diversity two or more times greater are the rule (Major and Bamberg 1967). On the other hand, it compares quite favorably with alpine floras in other parts of the Rocky Mountains and other North American ranges, e.g. the Rockies of central Montana with ca. 200 species (Bamberg and Major 1968), North Cascades with 250 species (Douglas 1973), Beartooth Plateau of Wyoming-Montana with 190 species (Johnson and Billings 1962). A serious problem in such comparisons, as Hrapko (1970) has recognized, is that "alpine" has been variously interpreted, so that one might unwittingly be comparing a species list of tundra vegetation with one that includes a goodly segment of forest.

Tundra communities in the Canadian Rockies

Tundra communities homologous with many in the Bald Hills have been described from various parts of the Canadian Rockies. The clearest correlations are in the Heath Group. Mountain heathers (*Cassiope*, *Phyllodoce*) are the most important low-alpine ground cover throughout the Canadian Rockies except toward the U.S. border (Baig 1972, Kuchar 1973) where

dry sedge meadows seem to replace them.

Cassiope tetragona, the most xerophytic of the heathers, is set apart in a distinct community type by Beder (1967), Hrapko (1970), Trottier (1972) and Knapik et al. (1973). *Phyllodoce glanduliflora* and *Cassiope mertensiana* are lumped into one community type (e.g. Hrapko 1970) or kept separate (Broad 1973, Knapik et al. 1973). In the Bald Hills the two were found together more often than not. *P. empetriformis* is not as abundant as the other heathers (in the areas thus far investigated), and a separate community type has not been erected for it. Trottier (1972) described a *Phyllodoce* association dominated by *P. glanduliflora, P. empetriformis* and their hybrid. Baig (1972) described two timberline community types co-dominated by trees and *Phyllodoce*. He considered the *Abies-Picea/ Phyllodoce* type the most widespread of all timberline types in the Alberta Rockies. This type would be the chief constituent of the forest-tundra zone.

Luetkea pectinata, a dwarf shrub dominant around timberline in mountain ranges west of the Rockies (Douglas 1972, Landals and Scotter 1974), is only locally abundant in the Rockies, e.g. at Mt. Edith Cavell in Jasper Park and in the Van Horne Range in Yoho Park (Kuchar unpubl.). It is restricted to sites with deep but not excessively late-lying snow.

Communities dominated by tall forbs have been described from the Canadian Rockies. Similar to the *Artemisia norvegica -Anemone occidentalis* type are Broad's (1973) NE-aspect

Anemone occidentalis-Thalictrum occidentale type and Knapik et al.'s (1973) *A. occidentalis* type. Broad's (1973) *Trollius-Caltha* community is similar to the *Artemisia norvegica/Salix arctica* type. I have seen small forb meadows in Yoho Park that belong to this type. Hrapko's (1970) *S. arctica* dominated communities are nearest the Herb Meadow Group. Trottier (1972) described three associations from Highwood Pass that are probably part of the *S. arctica* complex.

Artemisia norvegica is to the classification of Bald Hills vegetation what *Salix arctica* is to that of Signal Mt. Hrapko (1970) viewed *S. arctica* as the dominant and unifying species of her mesic group of communities, while I have seen *Artemisia norvegica* as characterizing the herb meadow communities of the Bald Hills. The Bald Hills are less xeric overall than Signal Mt., hence the lower cover of *A. norvegica* in the latter area. Interestingly enough, *A. norvegica* exhibits the broadest ecological amplitude of all apecies found on Signal Mt. (Hrapko 1970), whereas in the Bald Hills it is much more "nodal" (Fig. 14, Table 23).

A variety of snowbed communities have been described from the Canadian Rockies. Common to all studies is the *Carex nigricans* type. *Antennaria lanata* has been included in this community (Trottier 1972) or set off as a separate one (Hrapko 1970, Knapik et al. 1973). The *Luzula* snowbed type has apparently not been previously described. Common in some alpine tundra areas but not in the Bald Hills is an

extremely late snow-release community dominated by *Saxifraga lyallii* (Knapik et al. 1973).

Largest and most complex is the Stony Tundra Group (= Chionophobe group of Hrapko 1970). There seem to be four noda : (1) Communities in which *Dryas octopetala* and lichens are prominent : Beder's (1967) *D. hookeriana-Oxytropis podocarpa-Cetraria cucullata-C. nivalis* type, Bryant and Scheinberg's (1970) alpine fellfield, Hrapko's (1970) *Dryas*-lichen type, Trottier's (1972) *D. octopetala* association, Broad's (1973) *Dryas-Empetrum nigrum* type.

(2) Communities with high graminoid cover, especially of *Kobresia bellardii* (Beder 1967, Knapik et al. 1973).

(3) Communities on very exposed and unstable sites with minute plant cover chiefly of cushion forms, e.g. Kuchar's (1973) cushion-plant tundra type.

(4) Communities intermediate between Stony Tundra and other Groups, e.g. Hrapko's (1970) *Dryas-Salix arctica* type, Baig's (1972) *Abies-Picea/Dryas octopetala* type. Hrapko (1970) described a terracette community with *D. octopetala* dominating inter-terracette surfaces, and *Salix arctica, S. nivalis* and ericaceous shrubs on risers and bases.

Communities dominated by low willows, especially *Salix barrattiana*, are common in the Canadian Rockies (Beder 1967, Trottier 1972, Knapik et al. 1973, Kuchar unpublished). They normally occur along creeks and other well-watered, relatively sheltered sites below timberline. They are absent or

poorly developed in areas where a constant moisture supply is not assured, e.g. most of the Bald Hills and Signal Mt.

Tundra communities in other regions

Western North American alpine tundra

The major unifying element of Canadian Rockies and far-western tundra communities is heaths, dominating the groundcover around timberline (e.g. Brink 1964, Douglas 1972). Tall herb meadows rich in forb and graminoid species are also important in coastal ranges (Kuramoto and Bliss 1970). Species common to the Bald Hills and coastal mountains may differ in ecology, as reflected in phenology. The flowering period recorded by Pojar (1974) for vascular plant species in a forb meadow in coastal alpine tundra in B.C. ranged from 5 days earlier to 40 days later than for the same species in a forb meadow stand in the Bald Hills (Fig. 15). The position of some species in the two phenosequences diverged; e.g. *Ranunculus eschscholtzii* flowered very early in the Bald Hills sequence but in mid-season on the coast.

Many tundra communities in the Cascades are dominated by graminoids (Douglas 1973). Some others, dominated by heaths or *Dryas octopetala*, can be referred to Bald Hills types. The *Carex nigricans* snowbed community is a very widespread one in western North America (cf. Cox 1933, Douglas 1973).

Southward (generally S of the Canadian Rockies), cryptogams are a much less significant component of alpine plant communities. Bryophytes and lichens are scarcely

mentioned by Bamberg and Major (1968) in Montana alpine sites. In a part of the Medicine Bow Mts in Wyoming investigated by Bliss (1956), the only important lichens were crustose saxicolous species, and mosses predominated only in meadows.

In the generally warmer, drier central and southern Rockies there is a paucity of lush forb meadows and a total absence of heath communities. *Dryas*-dominated vegetation, a conspicuous element of Canadian Rockies tundra landscapes, is a very minor type in U.S. mountains, mainly on some N and E-facing slopes (Hayward 1952, Kiener 1967, Benedict 1970). These sites are fairly dry, cool, and thinly snow-covered and in this combination probably best represent the upland alpine environment of the Canadian Rockies.

Tundra vegetation in the central and southern Rockies is dominated by forbs e.g. *Geum rossii* and graminoids e.g. *Kobresia bellardii, Carex elynoides, Deschampsia cespitosa* (Cox 1933, Hayward 1952, Johnson and Billings 1962, Bell 1974, Olgeirson 1974). Such alpine meadow associations are very unimportant in the Bald Hills, and raise the question, If graminoid meadow is the climatic climax of alpine tundra in Colorado (Billings and Mooney 1968), what then is the climatic climax in Canadian Rockies tundra?

Arctic tundra

The communities of the Bald Hills are physiognomically, floristically and ecologically most similar to upland arctic tundra types. Communities dominated by *Dryas octopetala* or

D. integrifolia have been described from Alaska (Hanson 1951, 1953, Gjaerevoll 1954), the arctic mainland of Canada (Britton 1966, Neal and Kershaw 1973), the Canadian Arctic Archipelago (Savile 1959, 1961, 1964, Barrett 1972), Greenland (Gelting 1934, Böcher 1963, Raup 1965, 1971), and northern Europe (Nordhagen 1955, Gjaerevoll and Bringer 1965, Kilander 1965, Rune 1965, Rønning 1969). In the northern part of the Canadian Arctic Archipelago, heath vegetation mainly of *Dryas integrifolia, Salix arctica* and *Cassiope tetragona* predominates in uplands (Babb and Bliss 1974). In many arctic areas the latter two are the main competitors of *Dryas* (Raup 1971). In northeast Greenland *Dryas* occurs in virtually all habitats but more abundantly on the drier sites, while *Salix arctica* dominates mesic sites (Raup 1965). Heath is the typical vegetation in W Greenland, and dominated by *Empetrum nigrum, Cassiope tetragona, Vaccinium uliginosum* and other ericads (Holttum 1922).

Cassiope tetragona, the most important arctic ericad, exhibits a similar relation to snowcover as in alpine tundra. In the High Arctic it often occurs on E and SE aspects where some but not a great deal of snow accumulates (Savile 1964), generally less than a meter (Barrett 1972). East of the Mackenzie Delta, Corns (1974) found *C. tetragona* most abundant at the base of slopes where snow lay longest. It is generally referred to as a snowbed species in the Arctic, but this is strictly relative. Snowbeds are so shallow in most arctic areas compared to many mountain areas, that

what is called a snowbed species in the Arctic may be a fairly good chionophobe in an alpine area.

Forb-rich herb meadows seem peculiar to mountain systems. The broad range of soil moisture, snow release conditions, snowbanks and other environmental relations does not obtain in the Arctic. In the High Arctic it is so cold and dry that not only herb meadows but also snowbed vegetation is considerably restricted in size and flora (Billings and Mooney 1968).

Most lowland plant communities in the Arctic are dominated by graminoids, mosses and dwarf shrubs (Bliss 1956, Barrett 1972, Babb and Bliss 1974). Such communities are small and local in mountain tundra, in sites of impeded drainage. Floristic and vegetational similarity between arctic lowland tundra and the Bald Hills or other "average" Canadian Rockies tundra areas may be very low. For example, a low-arctic area studied by Corns (1974) had some physiognomic equivalents (e.g. shrub-heath types, herb types), but floristic similarity was low : of the 46 important species listed by him, only 22% occur in the Bald Hills. All community dominants were species either not found or not dominant in the Bald Hills.

Böcher's (1963) classification of W Greenland vegetation exemplifies the thoroughness and detail in which European synecologists have treated tundra (and other) vegetation, and reflects their greater familiarity with it. In addition to the basic criterion of physiognomy, Böcher has subdivisions

based on (a) moisture relations and (b) geographical distribution.

European alpine tundra

Alpine tundra in central Europe is richer in species than Canadian alpine tundra (cf. Major and Bamberg 1967), is floristically rather dissimilar (cf. Schroeter 1926, Braun-Blanquet 1948, 1954), and unlike in community structure. The prevalence of dry herb and graminoid communities, together with the richer flora, is suggestive more of communities of the southern and central Rockies rather than Canadian Rockies.

Canadian Rockies alpine vegetation seems to correspond better to that of Scandinavia where heaths and *Dryas*-dominated communities are prominent. *Dryas*-sedge associations, especially with *Kobresia bellardii* and *Carex nardina*, are common in Scandinavia (Nordhagen 1955). The *Cassiope tetragona/D. octopetala* community type occurs in northern Europe, in sites with some snowcover as in the Bald Hills. The most important bryophytes in this association are *Rhytidium rugosum*, *Rhytidiadelphus triquetrus*, *Hylocomium splendens* and *Tomenthypnum nitens*. The last two are characteristic of mesic or meso-hydric sites in the Bald Hills and the first is limited to xeric stony tundra. Thus the correspondence between North European and Canadian *C. tetragona/D. octopetala* types is less satisfactory than would seem from dominants.

Snow pattern and substrate are considered primary

factors in differentiating major vegetational groupings in northern Europe. Gjaerevoll and Bringer (1965) divided the tundra vegetation of Sweden into chionophobous and chionophilous groups, and these in turn into calcicoles and non-calcicoles. Their chionophobous group includes three alliances, Empetrion, Myrtillion and Dryadion. Important species in the Myrtillion are heaths e.g. *Phyllodoce coerulea* and *Calluna vulgaris; Lycopodium alpinum* and *Sibbaldia procumbens* are two differentiating species. The Myrtillion evidently corresponds to my Heath Group. It does not correspond to Nordhagen's (cited in Böcher 1963) Phyllodoce-Myrtillion which includes *Cassiope tetragona* and *Dryas integrifolia*- dominated communities many of whose cryptogam species are shared with the *C. tetragona/D. octopetala* community type of the Bald Hills.

Gjaerevoll and Bringer's (1965) Dryadion is correlated with basic substrata, and is separated on this criterion from the Empetrion. Belonging to the Dryadion are some vascular plants of *D. octopetala*/lichen tundra, e.g. *Carex rupestris, Silene acaulis, Potentilla nivea, Draba nivalis, Carex nardina;* and some lichens e.g. *Caloplaca, Rinodina, Ochrolechia, Pertusaria.* The Empetrion has some vascular plant species and many important fruticose lichens of *D. octopetala* /lichen tundra, e.g. *Alectoria ochroleuca, A. nigricans, Cetraria nivalis, C. cucullata, Thamnolia vermicularis, Vaccinium vitis-idaea, Festuca ovina, Hierochloe alpina.* If the Dryadion and Empetrion were lumped as one alliance, it would correspond closely to the *Dryas* Subgroup of the Stony Tundra Group.

The interpolation of substrate creates difficulties in comparisons of European with Rocky Mountain vegetation. The Europeans evidently have something we do not, *Dryas octopetala* as a marked calcicole (Gjaerevoll 1963, Elkington 1971). In the Rockies it may be found on much more highly acidic substrata than reported from Europe. Although it can grow on basic substrata, its place in many limestone ranges is taken by *D. integrifolia*.

Other discrepancies arise with snowbed communities. Cryptogams common in extremely late melting snowbeds in Europe (Gjaerevoll and Bringer 1965), e.g. *Kiaeria starkei*, *Conostomum tetragonum*, *Anthelia juratzkana*, *Solorina crocea*, *Distichium capillaceum*, are common constituents of heath communities (Table 17) or other mesic sites in the Bald Hills. They do not occur in communities of the snowbed series except at the drier end. Either snowbeds in Europe are not as late-lying as in the Rockies or the species are adapted for much later release sites in Europe. The relative unimportance of bryophytes in alpine snowbeds in western North America may be due to the sharp transition from medium to deep snow: the dry ridge - late snowbank environmental gradient is much sharper here than in most of Europe (Billings and Bliss 1959, Billings and Mooney 1968).

6. GENERAL ECOLOGY OF *DRYAS OCTOPETALA*

TAXONOMY AND PHYTOGEOGRAPHY

The genus *Dryas* (dryad, mountain dryad, mountain avens), in the family Rosaceae, includes a Holarctic group of mat-forming dwarf shrubs that often dominate vegetation of xeric habitats at higher latitudes and altitudes. Porsild (1947) considered the genus very old, with its closest relatives in *Sieversia* (*Geum*). Linnaeus in fact originally named a *Geum* species *Dryas pentapetalum*. Kuznetsov (cited in Juzepczuk 1929) viewed *Dryas* as a high-mountain genus, derived from southwestern U.S. and Mexican shrubs in the genera *Cowania* Don. and *Fallugia* Endl. Juzepczuk (1929) on the other hand considered eastern Siberia, high in diversity of *Dryas* taxa, as the main centre of evolution of the genus.

Dryas traditionally has included three well marked species: *D. octopetala* L., described in 1753; *D. integrifolia* M. Vahl (1798); and *D. drummondii* Richards. ex Hooker (1830). *Dryas octopetala* s.l. is the most widely distributed of these, occurring across the Arctic and into temperate latitudes via the alpine zone of mountain ranges. In North America it descends to ca. 37°N latitude (Colorado), in Europe 39° (Greece, Armenia), and in Asia 34° (Japan) (Porsild 1947). Northward it extends as high as latitude 83°15' in Greenland (Christophersen cited in Hanson 1953), but is absent from the Canadian High Arctic. Throughout its range *Dryas* flourishes in what is commonly considered a harsh environment: gravelly,

poorly developed soils deficient in nutrients and moisture; high wind exposure; lack of much if any winter snowcover; diurnal temperature extremes. Although rarely encountered in milder situations, it can thrive in a virtually frost-free environment such as the west coast of Ireland (Webb 1962)

Dryas integrifolia is found in Greenland and North America, where it ranges from wooded tundra to High Arctic. Its southernmost limit is central Montana and isolated mountains in New Hampshire. Like *D. octopetala* it occupies windswept, rocky terrain at high altitudes in the mountains, but it also penetrates well into the Montane zone in Jasper Park. In the High Arctic it is one of the commonest plants, dominating the drier sites together with *Saxifraga oppositifolia* and lichens (Porsild 1964, Savile 1964, Svoboda 1974).

The present stronghold of *Dryas drummondii* is northwestern North America, from Alaska to Montana and Oregon. Isolated colonies in the Lake Superior region and Gulf of St. Lawrence suggest a former more extensive range. In contrast with the first two species, *D. drummondii* is restricted to middle and lower elevations where it is a true colonizer species, abundant and often virtually the only plant on alluvial gravel and recently deglaciated terrain. It also stands apart morphologically by virtue of its yellow, nodding, partly closed flowers. *Dryas octopetala* and *D. integrifolia* both have white, erect flowers that fully expand. Hybridization has been reported between *D. drummondii* and *D. integrifolia* (Rouleau 1956).

In 1929 Juzepczuk, in a generic revision of *Dryas* dealing mainly with Palaearctic forms, established two sections and four subsections and provided descriptions for ten new species. This, together with three species that he had described earlier plus two other species, increased the total for *Dryas* to eighteen. In 1947 Porsild concluded a study of *Dryas* in North America that upheld Juzepczuk's classification and added two species from the Alaska-Yukon region. Porsild observed that most of the species occupied land surfaces that were either never glaciated or had experienced local glaciation only. This is most interesting in view of his subsequent statement that "All seem well adapted to unstable soils such as fresh moraines, gravel bars of glacial streams and erosion fans and, therefore, do remarkably well in close proximity to glaciers."

The narrow-species concept of *Dryas* was based in large part on morphological criteria, of the leaf in particular, such as size, crenation, and presence/absence of various types of glands and pubescence. Hulten (1959) exposed some of these as poor characters, and relegated a number of the species to taxa of lesser rank.

Studying *Dryas* in Greenland, Elkington (1965) found a whole series of confusing intermediates between *D. octopetala* and *D. integrifolia*, which he explained as introgressive hybridization subsequent to immigration by *D. integrifolia*. But he concluded that the two should probably be retained at the species level because the geographical distributions were

different, and the ends of the morphological spectrum evidently distinct. In my own observations in Jasper Park, I have found the two usually separated edaphically, *D. integrifolia* on limestone and *D. octopetala* on acidic rock. Although they come into contact locally, e.g. in the Opal Hills of the Queen Elizabeth Ranges, they do not appear to hybridize. Malte (1934) reported a hybrid from the Alberta Rockies.

One of the species that Juzepczuk (1929) described was *Dryas hookeriana*, from the Rocky Mountains and Cascades. J.D. Hooker, first to study specimens of this plant, referred it to *D. octopetala*. Juzepczuk, however, set it apart primarily on the presence of stipitate capitate glands. Furthermore, *D. hookeriana* appears to be isolated from arctic populations of *D. octopetala* s.s. Hulten (1959) considered the difference between the two minor, and relegated *D. hookeriana* to subspecific status of *D. octopetala*. I have chosen to follow this treatment.

MORPHOLOGY

Dryas is a mat or cushion-forming dwarf shrub. It has a taproot as much as 4 m long (Gelting 1934), with ectotrophic mycorrhizae (Schroeter 1926). Large nodules have been reported for *Dryas octopetala*, *D. integrifolia* and *D. drummondii* (Tisdale et al. 1966, Lawrence et al. 1967, Elkington 1971). Adventitious roots commonly develop from the horizontal stems but are generally nonfunctional (Gelting 1934, Raup 1969). Extreme asymmetry of compression wood of the stem is normal

(cf. Schroeter 1926).

Dryas has sympodial-type growth. New shoot development is from buds in the axils of uppermost leaves, though buds from lower parts of the shoot often develop (Sørensen 1941). The shoots of *D. octopetala* form tightly appressed groups or fascicles which, in the Canadian Rockies, are very rarely well-spaced (Plate 15). The upper surface of the oblong-ovate, coarsely crenate leaves is strongly rugose, with wart-like excrescences or merely glandular-viscid; the lower surface is densely tomentose. Leaves are typically erect in windy or xeric sites but tend toward a horizontal position in mesic sites.

Good morphological descriptions of *Dryas octopetala* are provided by Jessen (1913), Sørensen (1941) and Hitchcock et al. (1955-69). Elkington (1971) has treated its ecological life history.

GROWTH AND DEVELOPMENT

Introduction

According to Tikhomirov (1963), *Dryas punctata* over-winters with green leaves. *D. octopetala* is said to over-winter with partly developed, inrolled leaves (Sørensen 1941), which expand in the first flush of spring growth or during the flowering period (Elkington 1971). The flowering period is June-July in arctic-alpine habitats and late April-May in coastal sites (Webb 1962, Elkington 1971). Maximum shoot elongation occurs after the main period of flowering

PLATE 15. *Dryas octopetala* in open-growth form, rare in the Canadian Rockies. Note individual fascicles and non-abscissed dead leaves.

PLATE 16. *Dryas octopetala* in the Opal Hills, Queen Elizabeth Ranges. The extreme dimorphism does not reflect any obvious environmental discontinuity.

(Elkington 1971).

Although the life cycle of *D. octopetala* is understood in general (cf. Elkington 1971), I wished to relate earlier findings, especially the sequence of leaf production, to the *Dryas* populations in the Bald Hills. I also wished to follow the phenology of *D. octopetala* and relate it to environment.

Methods

Concomitant with phenological studies of vegetation in the Bald Hills, I recorded dates of snow release, flowering, and fruiting in *D. octopetala*.

To study leaf production I selected mats in a variety of sites, most near the fire lookout. I identified specific fascicles and from May 1970 to October 1971 traced the fate of current and new leaves by measuring length and width of lamina, length of petiole, and noting type and degree of discoloration. This was also done for shorter timespans, between 1969 and 1972, in other sites.

Results and discussion

Phenology

At all sites, xeric to mesic, dormancy of *D. octopetala* is not broken until several days after snow release. There was no evidence of any leaf elongation or greening beneath snow or immediately following snow release. I am not sure what the mechanism is for break of dormancy in mats that are exposed most or all winter, but suspect that near-surface soil temperature may be the critical factor. In growth chamber

studies of *D. integrifolia*, Svoboda (1974) found that as leaf temperatures, initially slightly below freezing, were raised by 1°C increments every 1-2 days, CO_2 uptake did not start until the tenth day.

In most upland sites, dormancy of *D. octopetala* is broken in early to mid-May, and there is rapid development of the overwintering half-formed leaves (Fig. 20). In 1971, development in stand 3 (Table 15) began ca. 1-5 May. By 10 May, leaves at mat edges were fully expanded and the others were elongating.

The first *Dryas* flowers appear ca. 1-2 June, or a few days later in years of late snowmelt. The flowering peak is from 25 June - 5 July, with a deviation of one week in years of early or late snowmelt. Peak bloom is earliest in matfields on warm aspects and latest in heath-dominated sites. The flowering period is relatively short at any given site : from the onset of flowering, individual mats take 7-10 days to achieve peak bloom and a further 5-6 days for most petals to wither. Flowering tails off by 10 July but a few flowers carry on or develop later in the season. Total flowering period appears longest in xeric sites and compressed in mesic sites. In *D. punctata*, flowering duration is lengthened in colder than normal weather (Tikhomirov 1963).

D. octopetala fruit development takes 6 weeks in most *D. octopetala*/lichen communities, slightly longer in *D. octopetala/Polytrichum piliferum* and cool-aspect *D. octopetala*/ lichen communities, and about 8 weeks in *Cassiope tetragona/*

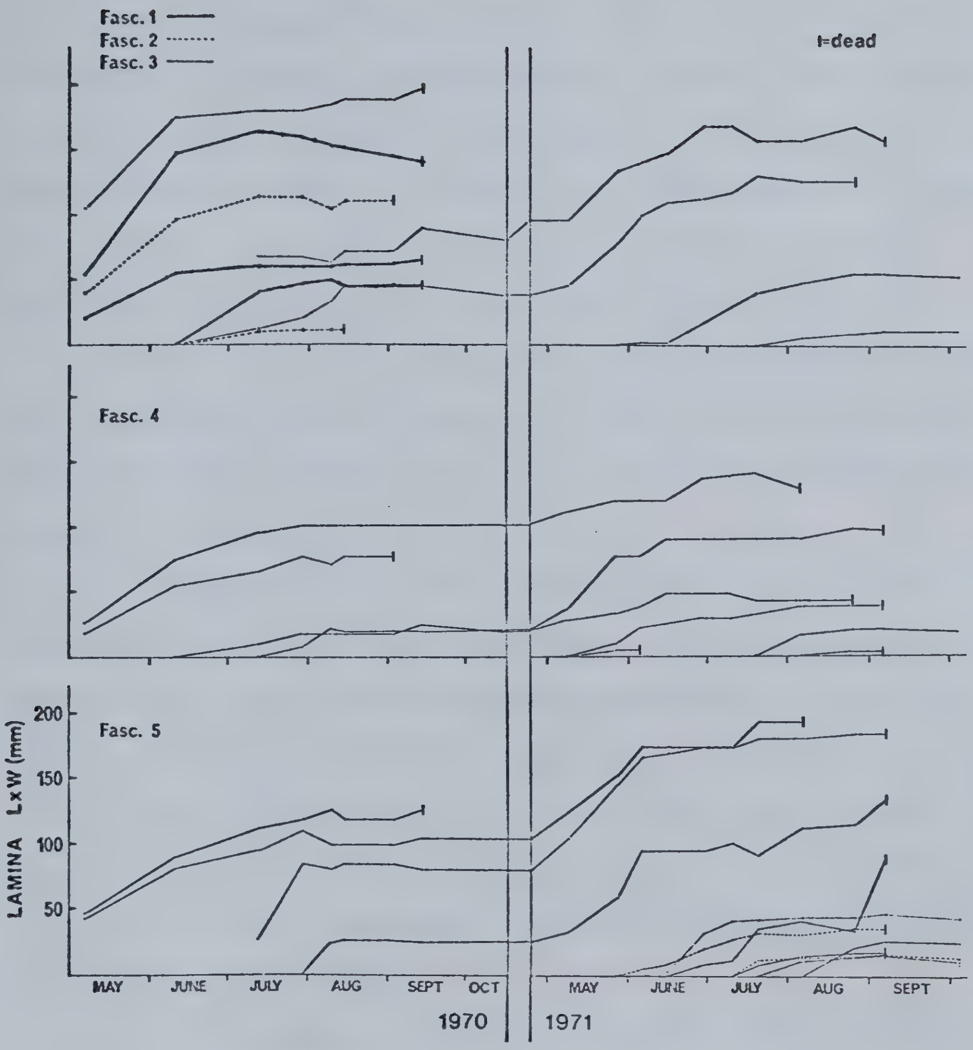


FIG. 20. Leaf development in five fascicles of a *Dryas octopetala* mat in a *D. octopetala*/lichen community, S aspect, near fire lookout.

D. octopetala and *Artemisia norvegica/D. octopetala* communities. Vegetative growth is probably favored in the mesic sites (cf. Holway and Ward 1963). Lower ground-surface temperatures may also be responsible for slower fruit development. Fruit dispersal in upland sites begins at the end of July and lasts almost a month. It begins 2-3 weeks later in *Cassiope tetragona/D. octopetala* and *D. octopetala/Polytrichum piliferum* communities, but only lasts about 2 weeks.

Gavriliuk (1961) reported a 40-day development period for *D. punctata* fruit in Siberia. Data from Devon Island (Svoboda 1974) indicate that *D. integrifolia* may take as little as 22 days to mature fruit.

In upland sites, the least affected by variations in snow accumulation and meltrate, dates of major phenological events of *D. octopetala* are comparable from year to year. Some relatively late-release sites may be as much as a month behind upland sites (Fig. 21). The latest date at which *Dryas* mats were still snow-covered was ca. 5 July 1968 in a *D. octopetala*/moss community. In 1969-72 this site melted out in early to mid-June.

Fall coloration, a slight yellowing or pink flush of the foliage (Plate 7), is synchronous between sites. In 1970 coloration began 20-25 August.

Leaf development

The development of *Dryas octopetala* leaves in an average *D. octopetala*/lichen community may be viewed in five

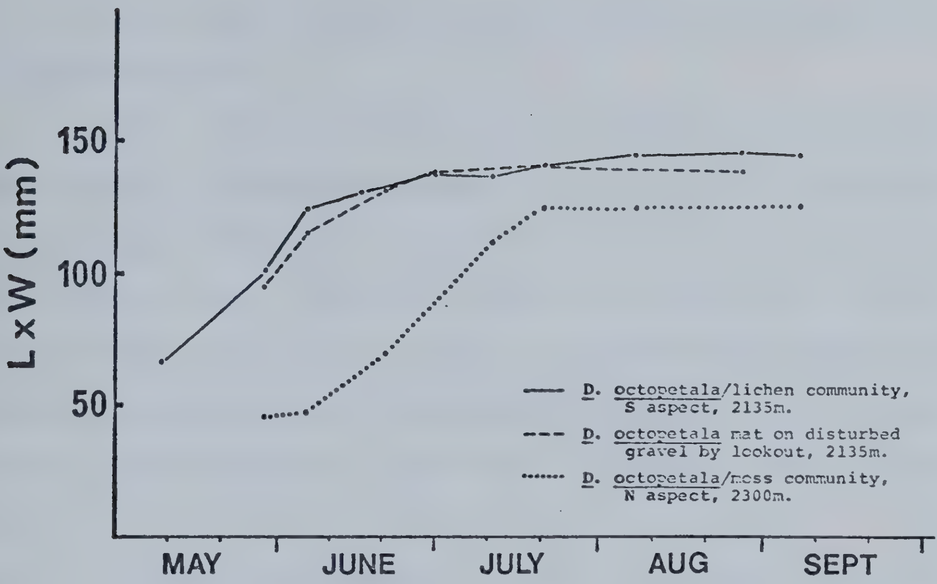


FIG. 21. *Dryas octopetala* leaf development, as mean length x width of 4-6 mature leaves, in mats at three sites, 1971.

stages.

(1) Growth of new leaves is brisk in the first 2-4 weeks, then normally ceases. Their emergence is staggered through the season (Fig. 20), with up to 10+ per fascicle by mid-August. Lamina size ranges from 2x1 to 18x6 mm, with petioles 0-10 mm long. Some or all of a fascicle's new leaves may die in the first season.

(2) All leaves overwinter in the form they have attained by mid-August.

(3) Rapid elongation and some broadening occur in May; an average lamina is now 15x4 mm. The leaves turn a dark olive color by September; some brown and become non-functional.

(4) The leaves overwinter without undergoing any changes in size.

(5) The laminae gradually elongate and broaden through May, sometimes through June, putting on up to 5x4 mm. Those leaves which were largest at the end of the first season are largest now. By mid- to late July they have a "dusty" green color (cf. Plate 16) due to numerous tiny wax plaques. The laminae may shrink fractionally in mid- to late season, turn a dirty yellow in late August, and then brown in September.

Gelting (1934) suggested that the lifespan of individual *D. octopetala* leaves in Greenland was 2-3 years. I did not study leaf development long enough to see if some leaves actually lasted three years. Studying *D. integrifolia* on Devon Island, Svoboda (1974) counted a mean of 2.6 functional leaves at the start of the season and 5 by early August. Bliss (1971) indicated that older leaves of most evergreen arctic-alpine species may not be very active photosynthetically, but act as storage organs whence lipids and proteins are translocated to new leaves each summer.

ENVIRONMENTAL RESPONSE AND ADAPTATIONS

Introduction

The pattern of leaf development in *Dryas octopetala* has obvious adaptive significance. *Dryas* grows chiefly in xeric upland sites with little snowcover. Rapid leaf maturation in spring takes advantage of the optimal growing con-

ditions at this time, with adequate soil moisture and abundant though not excessive heat.

Dryas has other foliar features of adaptive significance. Leaves form the primary contact with solar radiation, air temperature, and wind. Leaves in different sites should therefore vary, either through direct environmental stimulus or by ecotypic selection, or both. Transplant studies and leaf measurements are relatively simple methods of investigating these questions. Study of morphological parameters is certainly a simple and effective way to correlate plant response with site conditions.

Methods

1. Collections of live *Dryas octopetala* clones were made from 30 August to 3 September 1969. Altogether 131 clones were obtained from a wide variety of habitats in the Bald Hills. They were transported to Edmonton in open plastic bags, transplanted into clay pots using a 50:50 soil:sphagnum mix plus as much of the original substrate as possible, and put outdoors at the U. of Alberta Agriculture greenhouses where they remained for the next two years.

2. Eight clones from xeric habitats at middle alpine altitudes were transplanted to mesic sites near the fire lookout.

3. Of several hundred pressed *Dryas* specimens, I selected 50 from a range of habitats in the Bald Hills and a few from other parts of the Fockies. Each collection had to have enough material to allow a count of 25 mature leaves.

Measurements were made of length and width of lamina and length of petiole. Stipule length was measured in a few samples. Mean values were computed, along with length:width ratios of the lamina, and length ratios of lamina:petiole. An unsuccessful attempt was made to estimate degree of hairiness of leaf underside and degree of waxiness of upper surface.

4. I collected older stem parts (burls) from mats of *Dryas octopetala*, *D. integrifolia* and *D. drummondii* at several sites, counted and measured growth rings and computed mean widths.

5. At different times through 1969-71, at a number of *D. octopetala*/lichen and one *D. octopetala*/*Polytrichum piliferum* community, I took spot readings of : (a) temperatures near and within *Dryas* mats, using a Weston probe thermometer and a Yellow Springs telethermometer; (b) wind at different heights above and near *Dryas* mats, using a hot-wire anemometer; (c) short-wave reflectance off *Dryas* mats using a Stoll-Hardy radiometer, and global radiation (for albedo) using a Stern pyranometer.

Results and discussion

Live *Dryas octopetala* clones at Edmonton

Within a month of collection, 34 (26%) of the excavated *Dryas* clones were dead. Mortality was very low for the next two years in Edmonton. Nineteen (15%) of the clones flowered between 15-30 May 1970, and two flowers were seen on 2 July. The flowering period was thus about a month early in relation

to undisturbed clones. This further substantiates the idea that vernal response of *D. octopetala* is not innate-periodic as in e.g. *Trollius laxus*, but a direct response to environment especially temperature.

Only three of the plants that flowered did not set seed, indicating possible pollination by insects. Most of the plants appeared in good condition, with leaves in the typical near-upright position, but lacking wax secretions.

Although all clones were subjected to essentially identical winter conditions, flowering was not entirely synchronous. There was no evident correlation, however, between flowering date in Edmonton and original habitat in the Bald Hills.

The following year (1971) all plants were dead. A number of factors might be responsible, the most likely of these being (1) inadequate root collection and (2) very warm and long summer, causing respiratory depletion of food reserves.

Transplants

Transplant studies in the field failed. I had hoped to see an increase in leaf size when the xeric-habitat clones grew in the mesic site. Instead, the leaves reddened and the clones expired by the end of the following summer. Inadequate care with the taproot may have been the reason.

Leaf parameters

Leaf data are presented in Table 26. Mean length of

TABLE 26. Mean and 95% confidence interval of 25 measurements of leaf parameters, of *Dryas octopetala* mats collected in the Bald Hills and other Alberta localities. All measurements in mm.

LOCALITY & VEG./HABITAT	ALT. (m)	ASPECT & DEG. SLOPE	MAT NO.	LAMINA			PETIOLE LENGTH	LAMINA: PETIOLE
				LENGTH	WIDTH	L:W		
Bald Hills								
Dryas octopetala/lichen (matfield).	2280	S5	1	12.6±0.8	6.1±0.4	2.08±0.06	8.6±1.1	1.1±0.1
			2	14.8±1.6	6.6±0.6	2.24±0.08	10.4±0.6	1.4±0.1
			3	11.5±0.8	5.6±0.8	2.06±0.08	9.3	1.3
			4	12.9±1.0	5.9±0.4	2.19±0.08	8.8±0.8	1.5±0.1
			5	12.6±0.9	6.2±0.4	2.04±0.06	8.5	1.6
			6	12.9±0.9	6.2±0.4	2.11±0.06	8.6	1.6
			7	13.5±0.7	6.3±0.4	2.14±0.06	9.4±0.8	1.5±0.1
			8	15.0±1.3	7.7±0.6	1.98±0.12	10.6±1.2	1.5±0.1
			9	12.7±0.7	6.1±0.4	2.12±0.10	9.7±0.9	1.4±0.1
			10	12.7±1.0	5.9±0.4	2.16±0.08	9.8	1.3
			11	12.3±1.1	5.9±0.6	2.10±0.08	10.4	1.3
D. octopetala/lichen community on exposed ridge.	2280	SW2	12	10.6±0.8	5.5±0.4	1.96±0.08	7.8±0.7	1.4±0.1
			13	12.5±0.9	6.7±0.6	1.88±0.08	9.5	1.3
			14	10.8±1.0	5.7±0.6	1.94±0.10	9.4±1.0	1.2±0.1
			15	13.0±0.8	6.4±0.4	2.04±0.04	9.7±0.8	1.4±0.1
			16	12.2±0.9	6.0±0.4	2.04±0.10	8.5±0.8	1.6±0.1
			17	10.8±0.8	5.3±0.4	2.06±0.08	8.3	1.4
			18	13.4±0.8	6.1±0.4	2.20±0.08	10.1±1.1	1.3±0.1
D. octopetala/lichen community.	2280	0	19	13.7±1.0	6.4±0.4	2.16±0.08	13.0±1.1	1.1±0.1
Kobresia bellardii community.	2350	S25	20	11.7±0.7	5.8±0.4	2.04±0.10		1.1
D. octopetala/*Polytrichum piliferum* community.	2100	0	21	13.0±0.7	5.9±0.4	2.22±0.10	10.3	1.3
Artemisia norvegica/*D. octopetala*	2250	S5	22	14.3±0.8	6.8±0.4	2.10±0.10	12.6	1.2
Artemisia norvegica/*D. octopetala*; under *Picea* krummholz.	2250	S5	23	14.3±1.1	6.9±0.6	2.07±0.04	14.7±1.4	1.0±0.1
Artemisia norvegica/*D. octopetala*; under *Abies* krummholz.	2250	S5	24	16.9±1.3	7.5±0.8		15.8	
Cassiope tetragona/*D. octopetala* community.	2150	E5	25	14.2±0.8	6.1±0.4	2.35±0.08	12.8±1.0	1.1±0.1
Cassiope tetragona/*D. octopetala* community.	2500	E30	26	11.7±0.9	5.6±0.4	2.08±0.10	10.7±1.0	1.1±0.1
			27	11.7±0.9	6.4±0.4	1.82±0.06	9.8±0.9	1.2±0.1
			28	13.4±0.9	6.8±0.4	1.98±0.08	14.1	1.0
			29	15.2±0.8	7.5±0.4	2.04±0.06	12.5±1.0	1.2±0.1
Steep unstable shale slope near timberline.	2040	SE35	30	15.4±1.3	7.0±0.6	2.22±0.10	14.0±1.3	1.1±0.1
			31	15.3±1.3	6.8±0.4	2.26±0.10	12.8±0.1	1.2±0.1
			32	14.3±1.1	6.9±0.6	2.07±0.04	14.7±1.4	1.0±0.1
D. octopetala-*Arctostaphylos uva-ursi*.	2100	W30	33	18.0±1.7	8.2±0.8	2.22±0.08	15.4±1.7	1.2±0.1
D. octopetala-*Arctostaphylos uva-ursi*; against rock.			34	19.2±1.6	8.2±0.8	2.35±0.14	19.5±1.8	1.0±0.1
Cliff ledge.	2100	W5	35	15.4±1.5	6.9±0.6	2.23±0.10	13.3	1.2
Cliff ledge with ungulate droppings.	2100	W5	36	18.3±1.3	8.9±0.8	2.07±0.06	17.2±1.4	1.1±0.1
Seral *Vaccinium scoparium*-heath; on rock.	2000	W30	37	18.2±2.2	7.5±0.9	2.41±0.12	15.2±2.0	1.2±0.1
On hummock in forb meadow.	2100	N3	38	21.7±1.6	8.8±0.6	2.48±0.10	17.2±1.1	1.3±0.1
In heath tundra.	2150	NE10	39	14.4±0.8	6.6±0.4	2.20±0.06	12.5	1.2
			40	16.8±1.0	7.5±0.1	2.24±0.06	15.7	1.1
Opal Hills, J.N.P.								
Shale slope.	2375	S30	41	14.0±0.8	6.3±0.4	2.25±0.08	11.6±1.1	1.2±0.1
Limestone rubble slope.	2350	W30	42	15.0±0.6	6.6±0.2	2.28±0.06	12.1±0.9	1.3±0.1
On limestone outcrop	2100	-	43	19.2±0.8	9.1±0.4	2.12±0.03	18.2±0.8	1.1±0.04
D. octopetala/*Myosotis sylvatica* community.	2275	W20	44	15.6±1.1	6.5±0.4	2.30±0.10	12.0	1.4
			45	15.6±1.2	6.7±0.4	2.31±0.10	14.9±1.0	1.1±0.1
On small outcrop in *Picea-Abies* forest.	2000	W5?	46	20.0±1.2	10.2±0.6	1.97±0.06	15.4±0.9	1.3±0.1
Coronet Cr. alluvial fan, Maligne L., J.N.P.								
Open *Picea engelmannii*/*Dryas drummondii* community.	1675	0	47	13.0±1.0	6.1±0.4	2.15±0.10	11.9±1.3	1.1±0.1
			48	15.5±1.7	6.8±0.6	2.24±0.14	12.8±1.6	1.3±0.1
Marmot Basin, J.N.P.								
Cassiope tetragona/*D. octopetala* community.	2200	E25	49	13.9±0.8	6.6±0.4	2.12±0.08	10.9	1.3
Signal Mt., J.N.P.								
Cassiope tetragona/*D. octopetala* community on mesic slope.	2020	N25	50	15.4±1.2	7.0±0.6	2.22±0.08	13.8±1.3	1.2±0.1
			51	14.6±1.0	6.9±0.4	2.11±0.08	13.6±0.9	1.1±0.04
			52	15.9±1.4	7.2±0.6	2.19±0.08	16.1±1.7	1.0±0.04
			53	16.8±0.9	7.5±0.6	2.26±0.08	17.9±1.3	1.0±0.1
			54	17.7±1.3	7.3±0.4	2.43±0.10	15.6±0.7	1.2±0.1
			55	16.8±1.0	7.0±0.4	2.40±0.08	14.7±1.0	1.2±0.1
West Castle, Crowsnest Forest Reserve.								
Cushion-rosette community on ridge.	2300	N10	56	13.2±0.7	6.3±0.4	2.09±0.10	14.2	0.9
Bovin Lake, Crowsnest Forest Reserve								
D. octopetala/lichen community.	2150	E15	57	12.6±0.9	6.4±0.6	2.00±0.12	11.3±1.2	1.2±0.2
D. octopetala mats of cliff slopes.	2135	N45	58	13.1±0.9	7.4±0.6	1.80±0.08	11.8±0.8	1.1±0.1
			59	13.3±1.1	6.4±0.6	2.08±0.18	13.6±1.1	1.0±0.1

NOTE: Confidence interval not given where <25 measurements taken.

lamina varied from 10.8 to 21.7 mm in mats from a wide range of habitats. Mean width of lamina ranged from 5.6 to 10.2 mm, and mean length of petiole was 8.3 to 19.5. The few free stipule segments that I measured were 2-4 mm long. Length: width ratios of laminae, and lamina:petiole length ratios, were fairly consistent between mats.

Leaf characters were comparable among mats from the same site. Note for example the consistently high lamina : petiole ratios in mats 1-11, and the significantly lower ratios in mats 50-55. A high or low ratio does not seem to correlate with any particular site charcteristics or with leaf size. The conclusion is that the populations represented by mats 1-11 and 50-55 are clonal.

Leaf length (both lamina and petiole, since changes in length are in tandem) can be correlated with site, especially wind exposure: in general the windier the site the shorter the leaves. Mats 1-18, 20 and 57 have short leaves and originate on exposed sites. In E Greenland, Gelting (1937) noted that *Dryas octopetala* on snowfree sites had small leaves (f. *minor* Hooker), whereas mats in snow-covered sites had big, well-developed leaves with only slightly revolute margins. The implication is that in more xeric sites, *Dryas'* response is to decrease as well as partially enclose the transpiring lower leaf surface.

The leaves of mat 24, under *Abies* krummholz, are significantly longer than those of surrounding tundra (mat 22) or *Picea* krummholz (mat 23). The ameliorated microclimate

within the *Abies* krummholz produced a positive response in *Dryas*. Changes in growth habit also occur. Under the tiny krummholz conifers in *D. octopetala*/lichen tundra, *Dryas* mats are loose, sprawling, and with the leaves tending to lie horizontally; whereas adjacent exposed sites have compact, cushion-like mats with tightly clustered erect leaves. Simple response to environment, rather than ecotypic differentiation, is inferred.

Wind cannot be the only factor affecting *Dryas* morphology. Note for example mats 33, 34, 37, 43 and 46 (Table 26). These have among the largest of all leaves that were measured. These mats grew in warm microhabitats. A combination of little wind and high heat increment might produce the greatest stimulus to growth. The leaves of mat 36, manured by ungulate droppings, did not reflect any unusual growth stimulus. Shoot production of *D. integrifolia* on Devon Island increased no more than 50% following application of N, P, or a combination of N+P+K (Babb and Bliss 1974).

Growth rings of *D. drummondii* are far wider (Table 27),

TABLE 27. Growth ring widths of *Dryas* burls collected in various parts of the Canadian Rockies.

SPECIES	NO. BURLS	AGE RANGE	RING WIDTH (mm)	
			MEAN	RANGE
D. drummondii	13	7-15	0.37	0.30-0.69
D. integrifolia	3	8-22	0.09	0.08-0.10
D. octopetala	32	7-66	0.18	0.08-0.30

and rate of mat expansion an order of magnitude greater than in *D. octopetala*. *Dryas integrifolia* has the narrowest rings and slowest mat expansion.

Stems of *D. octopetala* from mesic sites generally have greater annual xylem increments than those of xeric sites. The smallest recorded increments were from a mat on a shaly windswept ridge. A mat manured by ungulates had a mean xylem increment of 0.21 mm. Large numbers of ring-counts would be necessary for a good evaluation of plant response to environment.

Dryas octopetala has a very slow growth rate compared to sympatric mat-forming species (Fig. 22), but more rapid

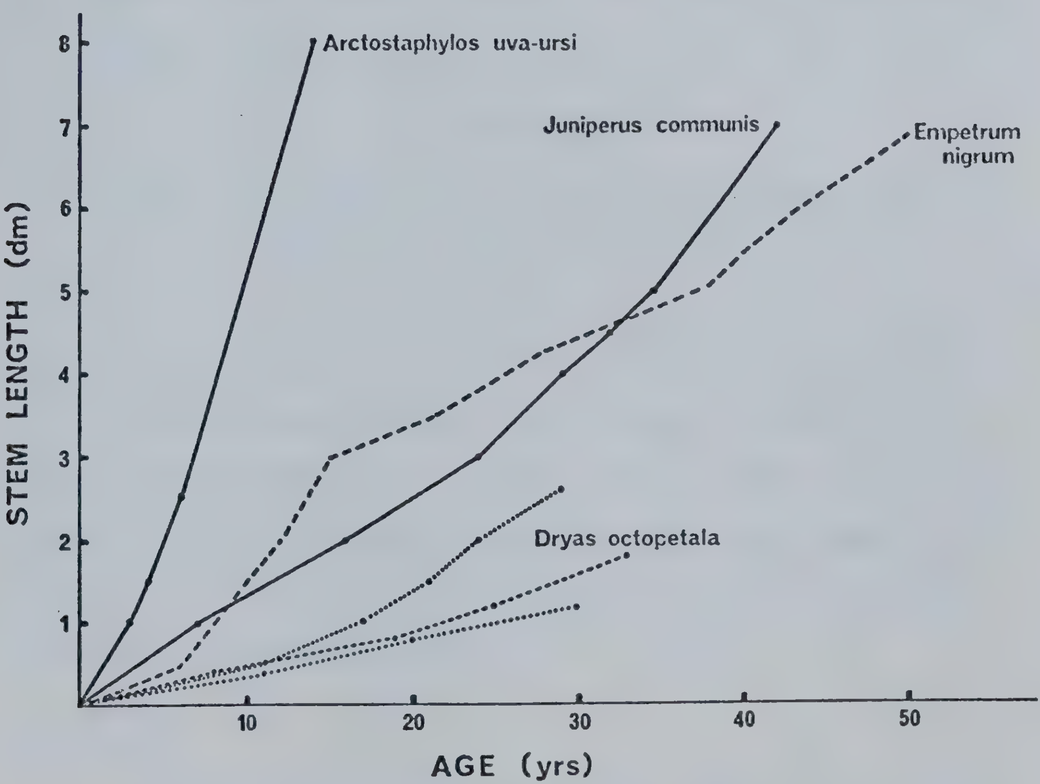


FIG. 22. Elongation rate in stems of four dwarf shrub species, on a steep SE-facing loose-shale slope at timberline. n=1.

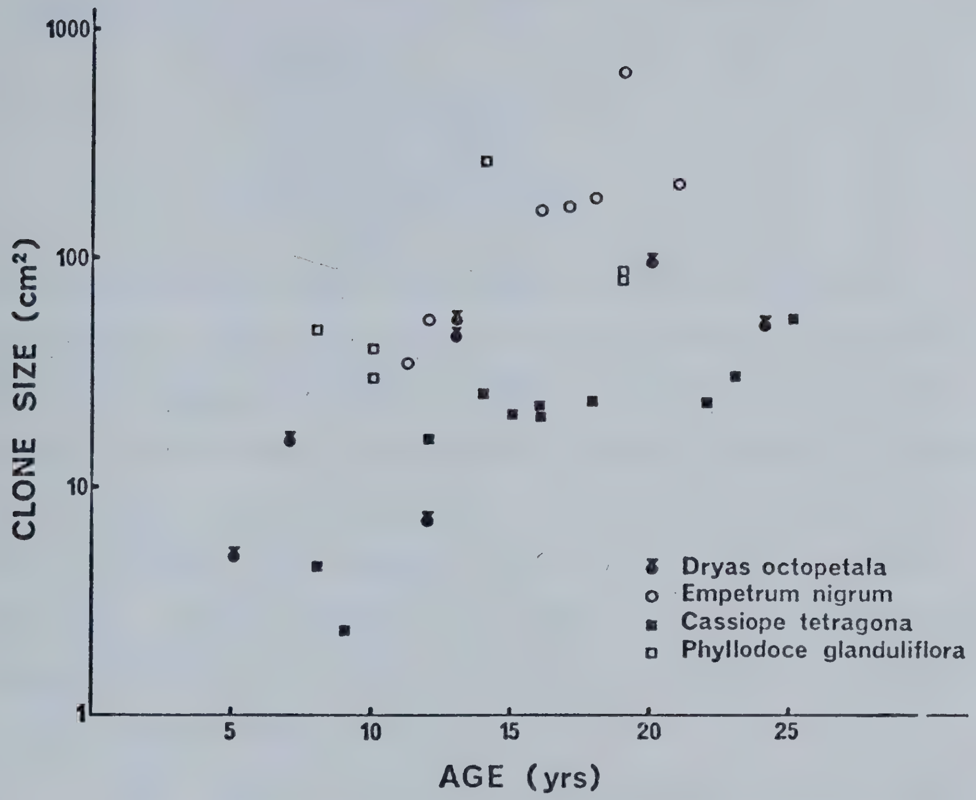


FIG. 23. Age-size relationship in four dwarf shrub species colonizing a disturbed SW-facing site at ca. 2250 m.

than heaths (Fig. 23). A conservative growth rate may be vital in xeric upland tundra where energy, nutrients and water supply are severely limited. But in mesic sites *D. octopetala* is handicapped compared to other mat species. It seems to have an initial advantage over heaths, but these can eventually shade it out.

Temperature

On sunny days there were large differentials between *Dryas* tundra surface and ambient temperature. On 7 May 1970

temperatures on a S-facing slope were as follows:

ambient	$9^{o}C$
D. octopetala mat surface	29
1 cm deep in mat	17
2 cm deep in mat	7
10 cm deep in mat	1
shale pebble surface	31
10 cm deep in shale	4

Spot readings at other dates and sites gave comparable gradients. *Dryas* mat temperatures were always higher than ambient, often by as much as $20^{o}C$. Adjacent unvegetated pebble surfaces were but slightly warmer than mats. In the High Arctic, leaf temperatures of *D. integrifolia* may be $20-30^{o}C$ higher than ambient (Mayo et al. 1973) or lichen and soil surface temperatures (Addison 1973). They are normally $5-15^{o}C$ above ambient during high sun hours (0600-1800) in the summer (Addison 1973).

Soil under *D. octopetala* mats was marginally colder than under unvegetated surfaces, indicating a slight insulating effect. In terracette *D. octopetala*/lichen communities the warmest microsites were bare terrace tops and the coolest were mossy hollows.

Wind

Mean windspeeds over *D. octopetala/Polytrichum piliferum* tundra at 1430-1500 hrs on 10 June 1970 were as follows:

1 cm above bare ground	0.71 m/sec
D. octopetala leaf-level	0.82
+2 cm	1.20
+10 cm	1.63
+50 cm	2.31
+100 cm	3.41

Windspeed decreases toward the surface, but is still

appreciable at the *Dryas* mat level. Deflation patches are common in the *D. octopetala/Polytrichum piliferum* community: fairly strong wind striking the edges of *Dryas* mats prevents development of total mat cover. Still, *D. octopetala* may be better suited for unstable windy sites than most other plants (cf. Bryant and Scheinberg 1970). In NE Greenland Raup (1971) found it the most stable species in dune areas where active deflation was occurring.

Albedo

Albedo values of *Dryas* mats in a *D. octopetala/ Polytrichum piliferum* community were ca. 15% looking straight down and ca. 25% when mats were viewed from an angle of ca. 30° to the horizontal and away from the sun. The albedo of *D. integrifolia* mats in the High Arctic is 13.8% (P.A. Addison *pers. comm.*).

When *D. octopetala* mats are viewed from the side while the sun is shining, they appear white due to the relatively high reflectance of the densely hairy leaf undersides. The leaves stand erect, arranged around shoot apices: the circle of white undersides reflects radiation and probably moderates heat buildup. The mature leaves may even curl back on themselves, forming over the immature leaves an umbrella which may reduce transpiration losses. Leaf orientation in *D. integrifolia* in the High Arctic is such as to preclude intolerable temperature rises (Svoboda 1974).

Other adaptations involving the leaves are glandular

secretions and the probable lack of stomata on the upper surface. Stomata have not been found on the upper surface of *D. integrifolia* leaves (Addison 1973). In early July the upper surface of many *D. octopetala* leaves develops a solid coating of a white waxy substance. This response may be temperature-induced, since it is especially prominent in plants adjacent to rocks.

7. *DRYAS OCTOPETALA* AND ASSOCIATED PLANT LIFE

INTRODUCTION

Parasites and saprophytes

A total of 26 species of fungi have been recorded on *Dryas* in North America and Greenland (Conners 1967). All but four are Ascomycetes, and most are saprophytic on dead leaves. Six have the specific epithet "*dryadis*" and, like the monotypic *Isothea rhytismoides*, may be host-specific.

Widden et al. (1972) studied fungal succession on *Dryas integrifolia* on Devon Island. They separated leaves into 5 classes: (1) living green, (2) brown, (3) brown with grey cast, (4) grey, (5) grey and starting to fragment. The leaves were cut into 2 mm segments and plated. There were no real differences in frequency of invasion or total numbers of species from one stage to another. Successional patterns were not as marked as in *Carex stans*. Ca. 24 fungal species were recorded on *Dryas*, compared to 18 for the sedge.

Other plants

Most ecological studies of *Dryas* stress phytosociological or autecological relationships. The few studies that deal with dynamics (e.g. Anderson 1967, Lawrence et al. 1967) may understate the significance of *Dryas* for other plants, or their precise spatial interrelationships.

In Spitzbergen, Rønning (1965) found crustose lichens thriving on *D. octopetala*. On Beartooth Plateau, Wyoming-Montana, Johnson and Billings (1962) found small matfields

of *D. octopetala*: "The mats have colonized wind-eroded areas and in turn are being invaded by various Geum turf species in the manner reported by Griggs (1956) for fell-field cushion plants in Colorado".

Preliminary perspective in the Bald Hills

In 1969 and 1970 I looked at spatial relationships between *Dryas octopetala* and other plants. There was very scant evidence of attack by pathogens, and I did not follow this line of investigation. Epiphytic relationships were also very rare - I found one instance of the crustose lichen *Rinodina pyrina* on old *Dryas* wood, and several cases where the fruticose lichen *Cornicularia aculeata* was attached to *Dryas* stems. There was, on the other hand, copious evidence that *Dryas* mats were being used as colonization sites by vascular plants and cryptogams. My hypothesis was, then, that in at least some communities *D. octopetala* was important, possibly critical to the survival of some plant species.

I looked for *Dryas*-dominated communities in fairly xeric sites, particularly those in which it formed a dominant but discontinuous cover of discrete mats. Here it has greater potential to benefit other plants - in mesic sites it might actually be a hindrance by competing for space or other resources. Also, for obvious reasons it is much more difficult to pick out interrelationships in a reticulate or closed mat cover. My quadrat data from the community analysis (Table 14) barely sufficed for a χ^2 test of association. Even highly significant correlations between *Dryas* and various

other species have relatively limited value: they only suggest association without specifying age, size, spatial relationships, or type of interaction.

Since *D. octopetala* was the most abundant upland plant, one would logically suspect it to be the most significant entity in the establishment and maintenance of populations of associated species. There are mat analogues such as *Salix arctica*, as well as cushion, rosette and tussock-forming species that may support other plants. One of the best-known of these is the ubiquitous arctic-alpine cushion plant, *Silene acaulis*. In Italy Whitehead (1951) found that in some alpine communities it provided a most important substrate for some vascular plant species. The most detailed studies along this line were by Griggs (1956) in Colorado, where he recognized the invasion of *Silene* cushions by many vascular plant species. In the literature on arctic-alpine vegetation, there are numerous cursory references to *Silene* cushions with plants growing on them.

METHODS

In August 1970 I evaluated a number of sites suitable for quantitative analysis of interrelationships between *Dryas octopetala* and other plants. I also considered sites that had *Silene acaulis* and *Salix arctica*.

Two intensive sites were selected on these criteria: (1) stand wider than 25 m and covering an area greater than 1600 m^2; (2) *D. octopetala* abundant as discrete mats; (3) no

sharp clines in plant distribution or abundance; (4) no sharp gradients in physical environment. A 1600 m^2 plot was staked out in each stand. The first (B1), 40x40 m, was on a 20^{o} SE-facing slope of loose shale pebbles with some conglomerate rocks. The second (B2), 20x80 m, was on a shaly E-W trending ridge. Each plot was divided into four 20x20 m subplots, and these partitioned into 2x2 m quadrats. Using a random numbers table, 100 of the 400 quadrats were sampled as follows:

(1) Plants of every recognizable species except saxicolous forms were enumerated.

(2) Diameter or lxw of each plant of *Dryas octopetala*, *Silene acaulis* and *Salix arctica* was measured.

(3) The dead percentage of each *Dryas* and *Silene* plant was estimated.

(4) A number of *Dryas* burls were collected for age determination.

(5) All instances of positive association between plants were noted. For *Dryas* and *Silene* the association was noted by zone: for *Dryas*, plants (a) near the mat (within ca. 2 cm), (b) within the outer actively growing portion, (c) in residual organic matter and old leaf-bases, (d) on mineral soil within the mat; for *Silene*, plants (a) near the cushion (within ca. 1 cm), (b) in the outer half-radius, (c) on the central portion. Crustose lichens were underestimated somewhat, since it was very difficult to detect minute clones.

I also selected a shale-pebble hillock populated with *Silene acaulis* cushions. A 10x7 m plot was staked out and

its macroscopic plant life inventoried. Diameter of *Silene* cushions was measured, and all associated plant species noted, by cushion zone.

To facilitate interpretation of the data, these two assumptions were made: (1) The interaction between individual plants is commensalistic[1]. There are, to be sure, instances of interaction that would be better described as (a) parasitic, one plant decreasing its host's efficiency; (b) competitive, both members of the association weakened; (c) mutualism, both members benefiting, usually due to greater stability *vs* erosion. But in general the associations should be viewed as "epiphytic" (Huntley 1971), i.e. a form of commensalism. (2) The relationship between any two species is unidirectional (Griggs 1956). For most species in the Bald Hills study, their role as host or commensal is quite obvious in all instances of association. The role of a few species is not obvious in a few instances of association; however, most instances subtend a clear chronological priority of one species, therefore we assume the uncertain instances of association to be of the same type (Griggs 1956). The one exception is in instances of obvious reversal of the relationship, e.g. a *Dryas* seedling associated with a large clone of some other plant. In his discussion of the problem of priority, Griggs (1956) mentions position, size and age as useful criteria. He also recognizes that an

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1 "In commensalism, one species does better, and the other does neither better nor worse. The one that does better is called the commensal, and the unaffected species is the host." (Malcolm 1966).

apparent "invader" might have been subsequently surrounded through strong radial growth by the "host". There is no firm evidence that the important host species in the Bald Hills employ encircling tactics.

ECOLOGICAL SPECIES-GROUPINGS

To paraphrase Watt (1947), I am here attempting to describe the plant community not from a diagnostic and classificatory viewpoint (as in Chapter 5), but as a working mechanism. I have classified the plant life of the study plots on the basis of spatial relationships, from which I may deduce type of interaction (and role). There are three groups. (1) Non-associative plants.

(a) Saxicolous cryptogams. In stand B2, saxicolous lichens - *Hypogymnia intestiniformis*, *Alectoria pubescens*, *Cetraria commixta* and crustose species expecially of *Rhizocarpon*, *Lecidea* and *Lecanora* - formed a fairly uniform cover of ca. 10%. The group was present in only trace amounts in B1. Saxicolous lichens and mosses (*Grimmia*) comprise an "inactive" group of plants. There is total negative correlation between these and other plants: wherever the latter grow the former are excluded.

(b) "Inactive" vascular plants. *Salix nivalis*, *Campanula lasiocarpa*, *Cerastium beeringianum*, *Stellaria longipes* and a few other vascular plant species are rarely found associated with other plants (Tables 28,29). Like the saxicolous lichens they are evidently autonomous in

TABLE 28. Interrelationships of plants in 100 1x1 m quadrats on a SE-facing shale-pebble *Dryas octopetala* matfield (stand B1).

SPECIES	TOTAL NO. PLANTS	NO. NON-COMMENSAL PLANTS	IN COMMENSAL ROLE: NO. IN *DRYAS* MATS	IN COMMENSAL ROLE: NO. WITH OTHER PLANTS	IN HOST ROLE: NO.	IN HOST ROLE: TOTAL NO. COMMENSALS HARBORED	IN HOST ROLE: MEAN NO. COMMENSALS/ HOST PLANT
VASCULAR PLANTS							
Campanula lasiocarpa	27	23	1	3	0	0	0
Carex phaeocephala	128	96	30	2	33	70	0.7
Cerastium beeringianum	17	17	0	0	0	0	0
Dryas octopetala	235	220	0	15	167	538	2.3
Festuca brachyphylla	128	80	42	6	6	8	0.1
Oxytropis campestris	44	32	12	0	1	6	0.2
Oxytropis podocarpa	120	95	25	0	1	4	0.0
Poa grayana	30	22	5	3	1	1	0.0
Potentilla diversifolia	81	68	10	3	21	41	0.6
Salix nivalis	89	60	28	1	6	9	0.2
Silene acaulis	12	9	2	1	5	7	0.8
Solidago multiradiata	14	6	6	2	0	0	0
Trisetum spicatum	26	12	11	3	0	0	0
other vascular plants[1]	54	38	12	4	0	0	0
BRYOPHYTES							
Bryum spp.	14	0	8	6	0	0	0
Ceratodon purpureus	13	0	9	4	0	0	0
Hypnum revolutum	89	5	35	49	5	7	1.4
Tortula ruralis	26	0	18	8	0	0	0
other bryophytes[2]	5	0	3	2	0	0	0
LICHENS							
Cetraria cucullata	45	0	42	3	0	0	0
Cetraria ericetorum	126	1	121	4	0	0	0
Cornicularia aculeata[3]	23	0	21	2	0	0	0
Peltigera spp.[4]	57	0	42	15	0	0	0
Psoroma hypnorum	23	0	12	11	0	0	0
crustose species[5]	29	0	13	16	0	0	0
other lichens[6]	10	0	5	5	0	0	0

NOTE: Listed are only those species occurring in 5 or more quadrats.

[1] *Abies lasiocarpa* (1 clone), *Agropyron latiglume* (1), *Anemone drummondii* (1), *Antennaria alpina* (7), *Arabis lyallii* (1), *Arenaria obtusiloba* (1), *A. rubella* (5), *Carex albonigra* (6), *Draba incerta* (5), *D. lonchocarpa* (3), *Eriogonum androsaceum* (10), *Luzula spicata* (3), *Picea engelmannii* (1), *Ranunculus* sp. (3), *Salix arctica* (1), *Saussurea densa* (1), *Stellaria longipes* (8), *Taraxacum lyratum* (2), *Poa lettermanii* (1), *Saxifraga bronchialis* (1).

[2] *Polytrichum* sp. (2), *Rhacomitrium canescens* (1), *Dicranum* sp. (1), *Rhytidium rugosum* (1).

[3] Low estimate?

[4] *P. canina*, *P. spuria*.

[5] *Caloplaca jungermanniae*, *C. sinapisperma*, *Lecanora castanea*, *Pannaria pezizoides*, *Rinodina roscida*, *Buellia papillata*.

[6] *Cladonia* cf. *chlorophaea* (1), *C. ecmocyna* (2), *C. pocillum* (1), *Collema* sp. (2), *Dactylina ramulosa* (1), *Stereocaulon alpinum* (2).

TABLE 29. Interrelationships of vascular plants in 100 2x2 m quadrats in a ridgetop *Dryas octopetala*/lichen community (stand B2).

SPECIES	TOTAL NO. PLANTS	NO. NON-COMMENSAL PLANTS	IN COMMENSAL ROLE					IN HOST ROLE		
			NO. IN *SALIX* MATS	NO. IN *DRYAS* MATS	NO. IN *SILENE* CUSHIONS		NO. IN OTHER HOSTS	NO.	TOTAL NO. COMMENSALS[1] HARBORED	MEAN NO. COMMENSALS/HOST PLANT
					dead	live				
Antennaria alpina	39	12	0	5	6	14	2	3	3	0.25
Arenaria obtusiloba	31	23	0	3	0	4	1	8	16	0.75
Artemisia norvegica	19	5	0	6	6	1	1	0	0	0
Campanula lasiocarpa	152	130	1	4	5	12	0	0	0	0
Carex albonigra	4	0	0	1	1	2	0	0	0	0
Carex phaeocephala	26	10	3	3	6	3	1	8	38	3.80
Cerastium beeringianum	43	39	1	1	0	2	0	0	0	0
Crepis nana	1	1	0	0	0	0	0	0	0	0
Draba incerta	68	35	0	5	5	14	9	4	11	0.31
Dryas octopetala	25	23	0	0	2	0	0	21	250	10.87
Erigeron aureus + E. lanatus	13	7	0	3	1	1	1	1	1	0.14
Festuca brachyphylla	25	12	3	7	2	0	1	4	11	0.92
Luzula spicata	39	4	0	7	10	14	4	4	8	2.00
Poa grayana	13	7	1	1	1	1	2	0	0	0
Poa lettermanii	148	105	5	3	2	26	7	10	22	0.21
Polygonum viviparum	4	0	0	3	0	1	0	0	0	0
Potentilla diversifolia	7	6	0	1	0	0	0	2	2	0.33
Potentilla hyparctica	187	127	1	6	8	38	7	52	135	1.06
Salix arctica	21	21	0	0	0	0	0	18	107	5.10
Salix nivalis	120	105	0	5	2	8	0	26	81	0.77
Silene acaulis	233	231	0	0	1	0	1	135	952	4.12
Stellaria longipes	16	13	0	2	0	0	1	0	0	0
Taraxacum lyratum	16	3	0	0	4	9	0	0	0	0
Trisetum spicatum	11	4	0	2	0	4	1	2	5	1.25

[1] Includes all lichens, bryophytes and vascular plants tallied in all non-commensal plants.

all parts of the life cycle. Their loose habit[1] and/or small size are not conducive to litter accumulation, therefore they rarely play a host role (Tables 28,29).

(2) Commensal species.

(a) Facultative commensal species. The majority of vascular plant species in the study plots (Tables 28,29) seem able to survive on a mineral surface, and even to germinate here in more stable microsites such as the lee side of rocks. However, most of these species appear to have taken advantage, in varying degrees, of the ameliorated microenvironment provided by host species. Facultative species exhibit a wide range in ability to harbor commensals.

(b) Obligate commensal species. These are species that are exclusively commensal; they include virtually all non-saxicolous lichens and bryophytes (Tables 28, 30, Appendix 8) and possibly a few vascular plant species e.g. *Luzula spicata* (Table 29). Under certain circumstances, e.g. in slight hollows or at the lee side of rocks, certain of these may survive without the assistance of other plants. It must be emphasized that many plant communities, e.g. boulderfields, have thriving populations of these cryptogams in the absence of hosts.

(3) Host dominants.

A very few species fall into this category. *Dryas octopetala* is the most abundant host species of upland

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[1] It was difficult to circumscribe individual plant limits for some of these species, especially *Campanula lasiocarpa* and *Salix nivalis*.

TABLE 30. Frequency of occurrence of commensal bryophytes and lichens in host plants in a ridgetop *Dryas octopetala*/lichen community (stand B2).

COMMENSAL SPECIES	TOTAL NO. PLANTS	NO. HOST PLANTS OCCUPIED				
		SALIX ARCTICA	*DRYAS OCTOPETALA*	*SILENE ACAULIS* live	*SILENE ACAULIS* dead	OTHER HOSTS
BRYOPHYTES						
Bryum spp.	43	2	3	27	4	7
Ceratodon purpureus	31	3	2	15	4	7
Dicranum scoparium	17	0	6	2	5	4
Hypnum revolutum	142	8	7	57	14	56
Lophozia s.l.	5	0	2	0	1	2
Paraleucobryum enerve	9	1	3	5	0	0
Polytrichum piliferum	41	2	7	14	10	8
Rhacomitrium canescens	100	11	13	27	15	34
Tortula ruralis	67	3	3	30	8	23
others[1]	9	1	4	2	0	2
LICHENS						
crustose spp.[2]	62	3	7	32	10	10
Caloplaca spp.[3]	81	7	5	37	15	17
Candelariella sp.	8	0	0	7	0	1
Cetraria cucullata	79	5	18	28	12	16
Cetraria ericetorum	95	8	17	32	11	27
Cetraria tilesii	8	1	5	0	2	0
Cladina mitis	4	0	1	0	3	0
Cladonia ecmocyna	46	3	4	22	8	9
Cladonia spp.[4]	57	1	5	30	9	12
Cornicularia aculeata	109	12	8	30	12	47
Dactylina arctica PD+	16	0	11	1	2	2
Dactylina ramulosa	37	4	1	10	6	16
Ochrolechia spp.[5]	38	1	2	16	6	13
Peltigera spp.[6]	93	6	10	40	14	23
Psoroma hypnorum	36	2	5	20	3	6
Stereocaulon alpinum	38	3	10	8	10	7
Thamnolia subuliformis	13	0	5	3	3	2
others[7]	7	1	0	4	1	1

[1] *Cephaloziella* sp., *Mnium blyttii*, *Ptilidium ciliare*, *Rhytidium rugosum*.
[2] *Rinodina mniaraea*, *R. roscida*, *R. turfacea*, *Buellia papillata*, *Lecanora castanea*.
[3] *C. jungermanniae*, *C. sinapisperma*, *C. stillicidiorum*.
[4] *C. coccifera*, *C. pocillum*.
[5] *O. frigida*, *O. upsaliensis*.
[6] *P. malacea*, *P. rufescens*, *P. scabrosa*, *P. spuria*
[7] *Collema* sp., *Lecanora verrucosa*, *L.* sp., *Solorina crocea*, *Stereocaulon subalbicans*.

tundra in the Bald Hills. *Dryas* mat analogues, notably *Empetrum nigrum, Arctostaphylos uva-ursi, Vaccinium vitis-idaea, Salix nivalis* and *S. arctica* are locally abundant. The last is the commonest, and stand B2 was chosen with it in mind. Species with rosette and cushion forms may be considered miniature mat analogues of *D. octopetala*. The commonest of these is *Silene acaulis*, and large populations are present in stands B2 and B3 (Table 29, Appendix 8).

Dryas octopetala, Silene acaulis and *Salix arctica* are called host dominants because they are superior host species: (1) they are abundant, and (2) they harbor relatively high numbers of commensals.

POPULATION STRUCTURE AND INTERACTION OF HOST DOMINANTS

All *Silene acaulis* cushions appear to be of seed origin - the plant has no apparent method of vegetative perpetuation. *Silene* seems a remarkably "free-living" species: only 6 of 380 cushions had of certainty originated in pre-established plants (Tables 28,29).

Dryas octopetala is well equipped for vegetative reproduction, but I do not know what % of the mats in B1 and B2 are of direct seed origin, and what % the result of mat fragmentation and rejuvenation. Twenty-seven seedlings were found; they were associated with other plants (12 instances), by stable rocks (2 instances), or a combination of the two (13 instances). On this basis *Dryas* might fall into the facultative category, but the ultimate significance of the

seedlings is not known: they are no guarantee of sexual success or necessity in mat population maintenance. In a *D. octopetala* community in Iceland, Anderson (1967) found no mats younger than 17 years. In his opinion all originated by separation of older clones into smaller, physiologically younger morphological units.

Scattered instances were seen, both in the study plots and other areas of the Bald Hills, of association between species of host dominants. This should not, however, be construed as evidence for some sort of cyclical successional relationship. Seedlings develop not on the vascular plant itself but on the organic substrate provided by the cryptogamic commensals in long-established hosts. In one case for example, I saw an old *Salix arctica* mat whose cryptogamic micro-community had a large *Silene acaulis* cushion on it. The *Silene* cushion's own cryptogam complex had a young but thriving *Dryas* plant.

In both *D. octopetala* and *S. acaulis*, the youngest plants in the study plots were the most numerous, with a sharp decline beyond 10-15 years. Assuming a stable population structure (and there is no reason not to), the data (Appendix 9) indicate: (1) high mortality of young plants; (2) no size/age range favored in *Silene acaulis*; (3) medium-young *Dryas* mats seemingly favored over other size/age classes. Svoboda (1974) figured a population of *D. integrifolia* clumps on a beach-ridge slope on Devon Island, in which the 100-200 cm^2 size (fairly small) was favored, whereas the

ridge crest had a steep death rate of small clumps.

There is an inverse relationship between numbers of plants in *Silene* cushions and % of cushion that is dead (Fig. 24), but this is not proof that larger numbers of commensals in the *Silene* cushion accelerate its death. The death of *Silene* cushions is greatest in the youngest age class, despite their freedom from commensals.

Few *Dryas* mats in the study plots (as well as most other areas of the Bald Hills) are more than 40-50 years old.

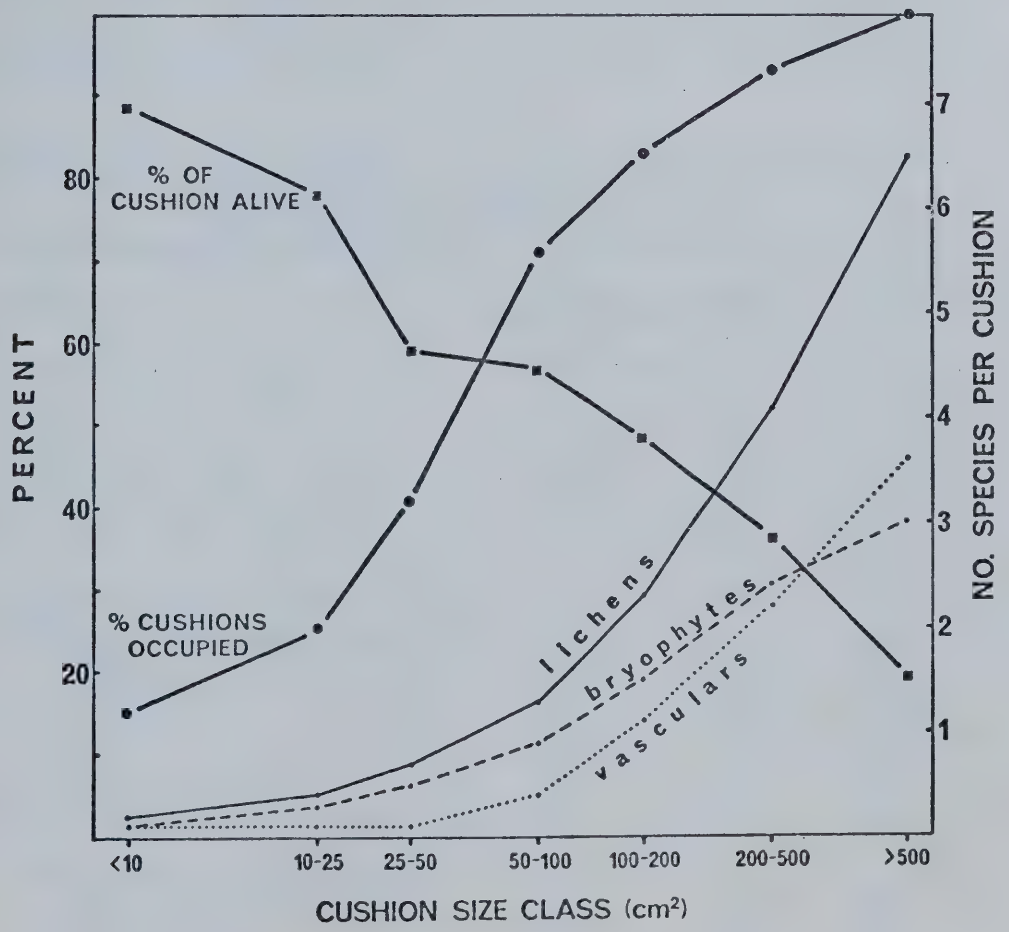

FIG. 24. Size, vigor and interspecific association of 239 *Silene acaulis* cushions in a ridgetop *Dryas octopetala*/lichen community (stand B2).

The actual clones could easily be hundreds of years old, but fragmentation and rejuvenation, or simply erosion of old wood, have disallowed large measurable ages.

HOST-COMMENSAL RELATIONSHIPS

Host species

The numbers of commensals in *Salix arctica* mats exaggerate its importance as a host. At 4 commensals per m^2 of host area (Table 31), it is an extremely poor substrate compared to *Dryas octopetala* ($38/m^2$), in turn much less

TABLE 31. Cover and plant associates of the three host dominants in a ridgetop *Dryas octopetala*/ lichen community (stand B2).

SPECIES	*DRYAS OCTOPETALA*	*SALIX ARCTICA*	*SILENE ACAULIS*
No. plants/400 m^2	25	21	241
% ground cover	1.78	6.47	0.77
Mean cover/plant (dm^2)	28.5	123.2	1.35
Largest plant (dm^2)	96	276	12
% plants with commensal spp.	84	86	59
Mean no. commensal spp./host			
vascular plants	3.0	0.7	0.9
bryophytes	2.4	1.5	1.1
lichens	5.5	3.0	2.1
total	10.9	5.2	4.1
No. species/m^2 host	38	4	250
Most species in one host plant	32	17	24
Total no. commensal spp.			
vascular plants	19	7	20
bryophytes	12	10	10
lichens	28	18	32
total	59	35	62

"efficient" than *Silene acaulis* (250/m^2). An average *Silene* cushion may cover only 1/10 the area of a *Dryas* mat yet harbor the same number of commensals; however, the mean area per commensal species is relatively small.

Salix arctica forms large but very loose mats. Litter accretion is minimal, and bare mineral surface is exposed throughout. In a number of mats the only commensals were *Cornicularia aculeata* and *Cetraria ericetorum*, attached to the woody stems.

Dryas octopetala provides a much better substrate. Its old leaves do not absciss and will only erode after many years. There is consequently more organic matter which, combined with the more compact growth form, provides a favorable microenvironment for other plants.

Silene acaulis forms an extremely compact cushion. Griggs (1956) noted invasion of *Silene* by large numbers of vascular plant species, which were somehow able to germinate and develop among the tightly appressed stems and leaves. For potential commensals the *Silene* cushion's only major drawback is its small size.

Other mat analogues in the study plots were not nearly so effective in a host capacity. *Potentilla hyparctica* was the most important of these (Table 29). Most graminoids were poor hosts, except *Carex phaeocephala* (Tables 28,29). Its relatively good host capacity is probably related to its larger (up to 100 cm^2) and longer-lived clumps.

Host size

There is a clear trend toward larger numbers of commensals in larger, older hosts (Figs. 24,25). While the potential host is small, the chances are relatively low that it will be contacted by propagules of potential colonizers. More importantly perhaps, a relatively rapid growth rate early in the host's life may produce an unstable substrate colonizable only with difficulty, particularly by slow-growing lichens. Young *Silene* cushions are uninhabited possibly because they are faster-growing. Allelopathy may also be implicated.

Most of the rosette and small mat species in the plots, even common ones like *Oxytropis campestris*, *O.*

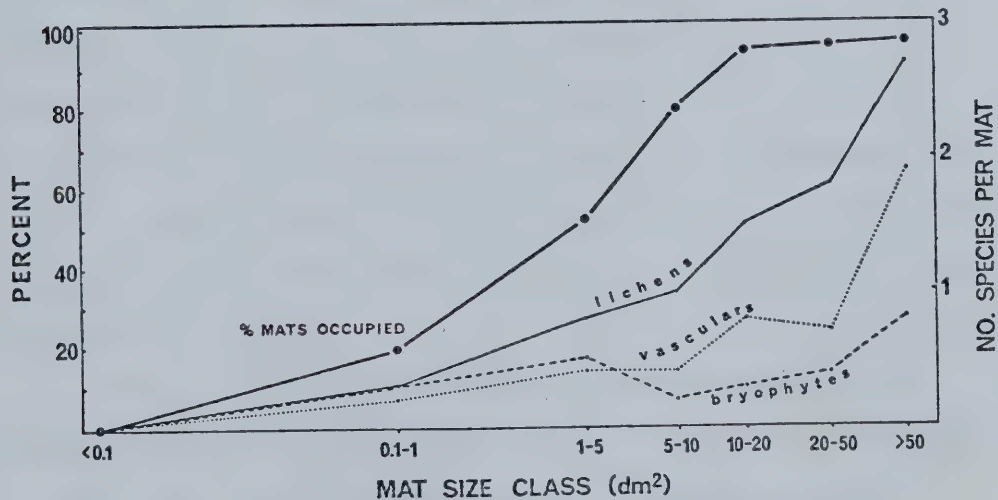

FIG. 25. Relationship between size and interspecific association in *Dryas octopetala* mats on a SE-facing loose-shale matfield (stand B1).

podocarpa (Table 28) and *Draba incerta* (Table 29), had very few commensals. There may be several reasons for this: (1) The hosts are small, therefore less likely to be contacted by colonizers. (2) Growth is relatively rapid over the entire plant surface. (3) The hosts are too small to produce any significant microhabitat changes.

Potentilla diversifolia and *Carex phaeocephala* were by far the best tuft-type hosts , probably due to their size: (1) they are relatively long-lived and stable; (2) they provide more colonizable surface than most other such species.

<u>Zone of colonization of host</u>

The distribution of commensals over the host surface is markedly contagious. Most commensals in *Dryas octopetala* mats grow on the residual organic matter which is in the central portion of most mats (but on the windward side of edge-eroding mats on some windy ridges). In graminoid hosts and the clump-forming *Potentilla diversifolia*, most commensals are at the edge. All parts of *Silene acaulis* cushions support commensals.

In any host, the metabolically most active part typically has the fewest commensals. *Dryas* mats have a 3-6 cm wide outer band of growing leaves in which commensal species are very rarely successful. In stand B2 there were 243 commensals in the central portion of the *Dryas* mats yet only 7 in the active leaf zone.

Tussock-forming and tufted plants have a very active

central zone where leaves and culms develop each year, and a very slowly expanding outer part. Commensals inhabit this outer zone and are restricted to it unless the host dies.

Vascular plants and crustose lichens were found more frequently in the central zone of *Silene* cushions (Fig. 26), despite the fact that this portion has only ca. half the area of the medial portion. Note the relatively high frequency of vascular plants at the cushion edge (Fig. 26). Their distribution is thus bimodal, high in the centre and at the edge, but low in the outer half of the cushion. In alpine communities in Italy, Whitehead (1951) found some vascular plant species consistently associated with *S. acaulis* cushions. Furthermore, some of the species consistently colonized the cushion edge while others the cushion surface.

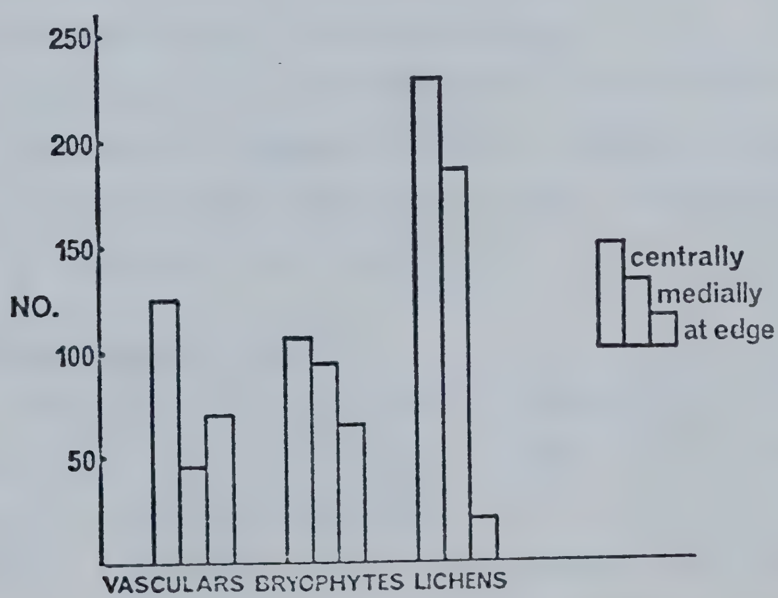

FIG. 26. Frequency of occurrence of lichen, bryophyte and vascular plant species in different parts of *Silene acaulis* cushions in a ridgetop *Dryas octopetala*/lichen community (stand B2).

Host habitat

Dryas octopetala mats are able to create a microenvironment distinct from but partly modified by the extrinsic habitat. In stand B1, mats are continually being infiltrated by shale pebbles, and they cannot provide commensals with the same degree of protection that they do on the B2 ridgetop, hence the low (2.3 *vs* 10.9) commensal frequency per mat. I have seen *Dryas* matfields in the Bald Hills and elsewhere with virtually no commensals because the mats had little control over the unstable substrate. At the other extreme are some later snow-release sites, e.g. the *D. octopetala*/moss community type, where mosses such as *Hylocomium splendens* and *Hypnum revolutum* grow so luxuriantly that only the leaf fascicles of *Dryas* protrude. Even the *Salix arctica* mats in these sites are thickly covered with mosses.

Colonization into *Silene acaulis* cushions seem relatively independent of general habitat. Unlike *D. octopetala*, *Silene* retains a compact form in all sites. Wherever *Silene* thrives it seems to harbor commensals.

Effect of commensals on host

Heavy colonization of hosts by vascular species could have an adverse effect by reducing already limited nutrient and moisture supplies. Mat hosts are much more frequently colonized by cryptogams, which do not compete for subsurface resources. Cryptogams are generally restricted to parts of the mat that are older and physiologically less active. By

colonizing senescing sections of a mat, they may actually be doing the host a favor, by accelerating the death of inefficient tissue that may be a respiratory burden. Fruticose lichens, common in older host plants, may lose water at a higher rate than does bare soil (cf. Addison 1973), and thus may create further stress on the host and possibly accelerate its fragmentation.

Tuft and tussock species are probably not adversely affected by most commensals except vascular commensals which however do not often colonize these hosts. Their active central area remains unaffected by peripheral cryptogam development. Indeed, a ring of tightly interwoven lichen and bryophyte clones may ensure greater stability by reducing needle-ice action at the tussock periphery. One common grouping in stand B1 was *Carex phaeocephala-Potentilla diversifolia-Hypnum revolutum*; the association of the two vasculars probably increased the chances of survival of all three.

Silene acaulis is probably the only host species whose death is likely accelerated by commensals (in which case they are not really commensals). It is readily colonized by many plants In Colorado, Griggs (1956) found it harboring more species than any other host. Heavy colonization by vascular plants is bound to weaken *Silene*cushions, through shading of leaves and competition for nutrients and water. Live cushions are also colonized by cryptogams, and it is difficult to see how there could be beneficial to *Silene*.

Host-commensal species correlations

Most commensal species showed no apparent host preferences. Some facultative commensals e.g. *Festuca brachyphylla* and *Artemisia norvegica* seemed to prefer *Dryas* over *Silene*, whereas others e.g. *Poa lettermanii* and *Taraxacum lyratum* showed a preference for *Silene* (Table 29). Some obligate commensals e.g. *Dicranum scoparium, Dactylina arctica* and *Stereocaulon alpinum* preferred *Dryas*, whereas others e.g. *Bryum* spp. and *Ochrolechia* spp. preferred *Silene* (Table 30).

There is some correlation between species of obligate commensal and host size, the larger commensals e.g. *Dicranum* and *Stereocaulon* confined to the larger host plants. *Cetraria* spp. and *Thamnolia subuliformis* are relatively more common in *Dryas* mats than *Silene* cushions possibly because, with their thalli attached to the substrate at only certain points, they are much more vulnerable to wind erosion on *Silene* cushions. Crustose species, on the other hand, cannot be dislodged by wind and are common constituents of *Silene* cushions. Substrate preferences might also explain some of the species associations.

COLONIZATION SEQUENCE AND SUCCESSION

Colonization of *Dryas octopetala*

The colonization of a growing *D. octopetala* mat may be reconstructed in five stages.

(1) The young plant, to 10-15 years old and 50 cm^2 in area, is very rarely colonized (Fig. 25).

(2) As the mat enlarges, the central portion gradually thins out, i.e. fewer leaves per unit area are produced. Crustose lichens appear, particularly *Caloplaca jungermanniae*. Some non-crustose species e.g. *Peltigera* spp. and *Cetraria ericetorum* may come in, as also one or two species each of mosses and vascular plants. The moss *Hypnum revolutum* may in a short while "homogenize" the habitat, creating a relatively uniform dense cover. Although it seems to discourage further moss colonization (cf. Fig. 25), the *Hypnum* provides an excellent substrate for lichens.

(3) With the mat covering 5-10 dm^2 and containing a well-established nucleus of commensals, another set appears, in large part utilizing the first as substrate. Established mosses, e.g. *Tortula ruralis* and *Hypnum revolutum*, are in some cases completely overtopped by crustose lichens. Established lichen thalli are colonized by other lichens, fruticose species e.g. *Cladonia* spp. and *Cornicularia aculeata* overriding crustose species, and other crustose species colonizing old or dead *Peltigera* thalli. A crustose lichen sequence may also occur. Mosses grow in openings among established lichens, and vasculars develop in cryptogamic micro-communities. The dead leaf bases of vascular commensals are colonized to a limited degree by crustose lichens.

(4) As the *Dryas* mat reaches 20-50 dm^2 and ca. 30-40 years old, the central portion becomes more and more open. Areas of bare mineral surface show through, and are

colonized to a limited extent by vascular plants and by *Polytrichum piliferum*. Most new additions to the mat microflora are still provided by lichens. Fruticose species begin to predominate on the stable cryptogam crust. This crust spreads onto mineral surface but, since it has no strong hold on the substrate, is still reliant on the encircling *Dryas* mat for protection against wind erosion. Watt (1947) described a sequence in which older parts of *Calluna* were colonized by lichens which eventually dominated, but were broken up by wind.

(5) Large (>1 m^2) intact *Dryas* mats are uncommon in the Bald Hills. Before they can reach this size they break up into clonal units that either rejuvenate or totally erode away. Most or all commensals are apparently lost. No mats were actually "caught in the act" of disintegration or rejuvenation. However, this is the only logical explanation for the present vegetational pattern, assuming that the vegetation is in a mature state. This is much easier to accept than the idea that the mats and remainder of the vegetation are precisely now beginning an inexorable spread culminating in a closed plant cover.

Colonization of *Silene acaulis*

Colonization of *Silene* cushions (Fig. 24) follows the same general sequence seen in *D. octopetala*, but the steps are more predictable since general habitat characteristics have very little influence on the commensal's substrate i.e. the cushion surface.

(1) Young cushions, up to ca. 50 cm^2, are very rarely colonized (Fig. 24).

(2) Crustose lichens, especially *Caloplaca* spp., begin to appear on the central portion of the cushion along with the first vascular commensals. *Hypnum revolutum* is usually the first bryophyte to appear, and may do so in any part of the cushion.

(3) Just as in *Dryas*, the next wave of colonizers play the role of "hyperparasites", developing on established lichens and bryophytes. A common configuration at this stage has *Hypnum revolutum* on the outer half of the cushion, patches of crustose lichens (*Caloplaca, Ochrolechia, Psoroma*) centrally on dead *Hypnum* or *Silene*, a few tufts of vasculars centrally or at the edge, and some small clones of fruticose lichens (*Cornicularia, Cetraria*).

(4) Medium-sized cushions (100-500 cm^2) acquire a set of lichens, mostly fruticose species, that colonize the stable cryptogamic crust. Some colonization by mosses also occurs. Vascular plants begin colonizing in quantity, mainly in the central portion of the cushion (Fig. 27).

(5) Large cushions (>500 cm^2) have a final wave of vascular plant colonizers. These occupy primarily the medial portion of the cushion (Fig. 27), which suggests a deteriorating ability of the cushion to exclude vascular plants, possibly because of decelerated growth-rate. Note the leveling off of numbers of colonizers in the cushion centre, implying saturation density of commensals.

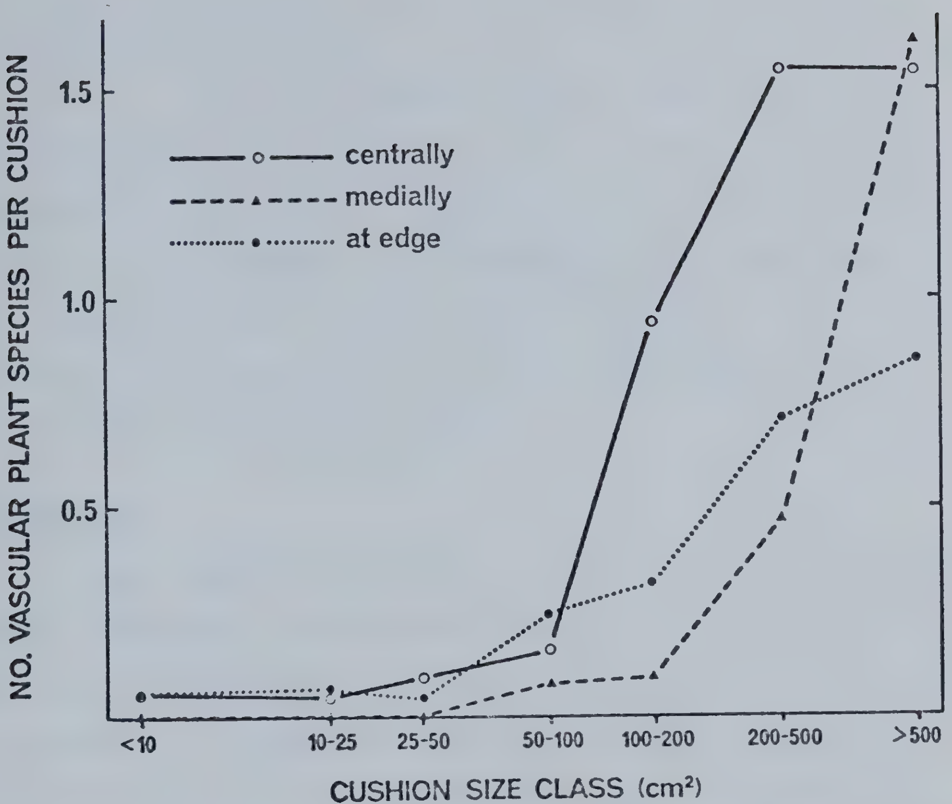

FIG. 27. Frequency of occurrence of vascular plant species in *Silene acaulis* cushions of different size classes, in a ridgetop *Dryas octopetala*/lichen community (stand B2).

(6) As the *Silene* cushion ages, the percentage dead surface increases (Fig. 24). It ultimately dies, and the built-up stems are completely covered by a layer of commensals. Some of the vascular commensals have by now attained a respectable size and may themselves be colonized. Most of the facultative commensals seem to prefer dead cushions (Table 29). *Potentilla hyparctica* and *Poa lettermanii* appear indifferent to host status. Most cryptogams also seem indifferent (Table 30); a few, e.g. *Stereocaulon alpinum*, show definite

bias for dead cushions.

(7) Unlike *Dryas*' terminal phase, where mat fragmentation and rejuvenation likely occur, the *Silene* cushions die and population replacement must come through seedling establishment. Disintegration and total erosion of the *Silene*-commensal complex must be assumed, otherwise it is difficult to account for the low total plant cover, particularly of non-host species.

<u>Succession</u>

The colonization sequences outlined above are by no means inflexible. There is a good deal of variability in pattern of colonization from one host plant to another. It is possible to discover almost any colonizer species in a host of almost any species or age. This diminishes the impact of the idea that biological succession is taking place.

Another reason why a successional sequence may be doubtful is this: In both the *Dryas* and *Silene* sequence most colonizers, even the earliest, hang on to the end. There is continual flux in relative abundances of commensal clones, but no real turnover. The only hint of succession is the decrease in mean numbers of bryophyte species in medium-sized *Dryas* mats (Fig. 25). The only truly successional event is the death and disintegration of the *Silene* cushion, or the fragmentation of the *Dryas* mat.

There is basically a three-phase cycle: host plants begin to develop, are colonized by commensals, and erode.

The estimated time of one cycle in *Dryas* is 50 years; I would guess 50-100 years in *Silene*. Since host plants are in all stages of development and colonization, the tundra will look about the same through the years. As Watt (1947) put it: "Although there is change in time at a given place, the whole community remains essentially the same."

In regeneration complexes studied by Coombe and White (1951) and Anderson (1967), several distinct successional steps were reconstructed. White (1951) described a 2-dominant cycle: *Silene acaulis* cushions were colonized by *Festuca dura* which persisted after the *Silene* eroded; *Silene* seedlings developed in the accumulated soil left by the grass.

8. *DRYAS OCTOPETALA* AND ASSOCIATED ANIMAL LIFE

INTRODUCTION

Invertebrates

Most studies of tundra arthropods stress environmental, temporal or taxonomic relationships. Few invoke vegetation and if so usually in a very general way. For example Hammer (1953) and Bohnsack (1968), working on tundra Collembola and general invertebrates respectively, implicated only three basic microsites, hydric, mesic and xeric. In a study of insects on Devon Island, Ryan (1972) compared meadow and beachridge catches.

Two investigations of flower-insect relations in the Arctic shed some light on *Dryas*-arthropod interaction. *D. integrifolia* was the dominant vascular species in the Lake Hazen, Ellesmere Island area (Savile 1964) where both studies were conducted. Hocking (1968) found that *Dryas* flowers were visited by many different flies and Lepidoptera and had a much higher value of grams total sugar per unit area than the next-best species. Kevan (1970) followed up these studies and identified 42 genera of arthropods in 21 families visiting *Dryas* flowers; it was "the most diversely visited flower". *Dryas* flowers also served as important microsites where, Kevan found, insects could rapidly warm themselves well above ambient temperatures. *D. integrifolia* benefited from the insect association: although it could set seed autogamously, it depended on insects for maximum seed set. Important pollinators were *Rhamphomyia nigrita* and *R. filicauda* (Empididae), *Eupogonomyia*

groenlandica, *Pogonomyoides segnis* and *Spilogona* spp. (Anthomyiidae), *Aedes* spp. (Culicidae), *Carposcalis carinatus* (Syrphidae), most Lepidoptera, and the bumblebee *Bombus polaris*. These, along with *Smittia velutina* (Chironomidae), *Boreellus atriceps* (Calliphoridae) and tachinid flies were the most important pollinators in the Hazen area.

Hocking (1968) noted very small noctuid larvae (*Sympistris labradoris*) in *D. integrifolia* flowers. There was usually only one per flower. It "fed rapidly, starting on the tissue between the nectaries and the ovary, but damaging both of these structures, and proceeding to eat out the whole of the ovary". Kevan (1970) found many flowers with the reproductive organs eaten out and only frass left, even in flowers not yet opened. Oliver et al. (1964) recorded several other, polyphagous lepidopterous larvae on *D. integrifolia* in the same study area. The larvae of *Anarta richardsonii* and *Lasiestra leucostyla* (Noctuidae) in the Canadian Arctic were most often collected on the commonest plants including *D. integrifolia* (MacKay 1972). On Bathurst Island, Danks and Byers (1972) found that larvae of *Psychophora sabinia* (Geometridae) would eat proffered *D. integrifolia* leaves. In Siberia, larvae of the geometrid *Cidaria caesiata* caused considerable damage to *D. punctata* fruit (Gavriliuk 1961).

Kevan (1970) recorded a spider mite (*Bryobia*) on *D. integrifolia* and crucifers. Richards (1964) described the mealybug *Pseudococcus (Chorizococcus) altoarcticus* from *D. integrifolia* in the Lake Hazen area. The aphid *Acyrthosiphon brevicornis* inhabits stems and leaf undersides of *Dryas* in

the Canadian Arctic (Richards 1963) and Greenland (Lambers 1960). Five species of moths with leaf-mining larvae have been recorded on *D. octopetala* in the Alps: *Tinagma dryadis* (Douglasiidae); two species of case-bearers (Coleophoridae), *Coleophora fulvosquamella* and *C. derasofasciella*; a fold-miner (Gracilariidae), *Parornix alpicola*; and *Stigmella (Nepticula) dryadella* (Nepticulidae) (Hering 1957). Pelham-Clinton (1967) recorded the last two, along with *Parornix leucostola* and *Epinotia mercuriana* (Eucosmidae), on *D. octopetala* in Scotland.

Compared to *Salix arctica*, its most important mat analogue, *Dryas* is relatively unscathed by parasites and phytophages. *Salix* is notoriously susceptible to attack by a wide array of leaf-miners, gall insects and other micro-consumers (Hering 1957, Buhr 1964, Kevan 1970). Oliver et al. (1964) found that *S. arctica* in the High Arctic brought together "a considerable and diverse group of insects that depend on it for food", at least twice as many species as on *Dryas* (excluding nectar and pollen feeders). Other mat analogues are much better off. *Empetrum nigrum* and *Silene acaulis* have only one gall-former each (Buhr 1964) and no miners. *Arctostaphylos uva-ursi* in Europe hosts four miners and 3 gall insects and *Vaccinium vitis-idaea* 7 miners and 3 gall insects (Hering 1957, Buhr 1964), but some of these are probably restricted to lower elevations.

In feeding experiments in Greenland, the plant bug *Chlamydatus pullatus* was given a choice of the nine commonest

heath tundra plants. It was recorded sitting on *Dryas integrifolia* in 11% of observations, yet only once seen to feed on it (Böcher 1971).

Vertebrates

Ptarmigan are the only birds known to feed on *Dryas*. Crop content analysis of 286 white-tailed ptarmigan in Colorado indicated light utilization of *D. octopetala* leaves in winter and spring (May and Braun 1972). In east Greenland Gelting (1937) observed that when heavy snowfalls precluded *Salix arctica* as a food source, ptarmigan would shift to *D. octopetala*. As many as 5000 leaves were found in one crop. Willow ptarmigan in Alaska include small amounts of *D. integrifolia* leaves in their diet in fall and spring (West and Meng 1966). *Dryas octopetala* is an important spring food of tundra ptarmigan in the U.S.S.R. (Aleksandrova 1964). A common Russian name for *D. octopetala* is "ptarmigan grass".

Willow Ptarmigan and arctic hare *(Lepus arcticus)* on Ellesmere Island were recorded eating *D. integrifolia* flowers (Kevan 1970). In winter the plant is utilized by lemmings (Aleksandrova 1964, Speller 1972). It and other plant species seem to be utilized in proportion to their abundance. Young leaves and flowers are eaten by reindeer (Aleksandrova 1964). The leaves are used as a tea substitute, or even as food, by Eskimos in Chukotk (Aleksandrova 1964).

Exclosure studies in Scotland indicate that intense grazing, mostly by sheep but also by rabbits, may eliminate *D. octopetala* and induce herb-rich grassland (McVean and Ratcliffe cited in Elkington 1971). Grazing changes the mat

from vigorous, long-leaved and many-flowered to short-leaved, few-flowered, and slow-growing.

METHODS

Through the 1968-70 seasons, as well as in short winter and summer trips in 1969-72, I took notes on bird and mammal activity in the Bald Hills, and related animal distribution to habitat and community types. I also studied plants of *Dryas octopetala* for evidence of utilization.

The invertebrate fauna was treated in six ways.

1. *Dryas* phytophagy was investigated by collecting leaves and flowers and scrutinizing these for abnormal coloration, swellings, excisions, and presence of arthropods. Some leaves and flowers were viewed *in situ* for presence of mites and other micro-arthropods. One 17x10 cm mat was collected on 3 Aug 1970 and all leaves examined at the field-lab. Activity of known *Dryas* phytophages was also inferred from other sampling procedures, treated below.

2. I noted instances of bumblebee/flower interaction, and fly and butterfly visits to *D. octopetala* flowers; but no intensive pollination studies were undertaken.

3. The 1.4 liter tins used to measure precipitation also trapped some flying insects, mostly flies. I transferred these to 70% alcohol, and related species and numbers to site and date.

4. Specific relationships of arthropods to *Dryas* tundra microsites were investigated through pitfall trapping.

Selected were an "average" *Dryas octopetala*/lichen community with solifluction terracettes, a xeric *D. octopetala*/lichen community, two *D. octopetala*/*Polytrichum piliferum* communities near conifer clumps, a *Cassiope tetragona*/*D. octopetala* community, and a high-alpine *D. octopetala*/lichen community. In 1970 34 traps were maintained, decreasing to 27 traps for two *Dryas*-dominated community types in 1971 and 29 traps in 1972 (Table 32). In 1972 I also monitored a transect of nine

TABLE 32. Numbers of pitfall traps set out in the Bald Hills.

VEGETATION TYPE	1970	1971	1972
Dryas octopetala/lichen	19	19	27
D. octopetala/*Polytrichum piliferum*	10	3	0
Other *Dryas*-dominated tundra	5	5	2
cushion-rosette	0	3	3
heath	6	0	6
forb meadow	5	3	0
snowbed	6	0	0
others	7	0	0
TOTAL	58	33	38

traps in *D. octopetala*/lichen tundra, from shale-pebble to conglomerate surface. In 1970 only mid- and late-season arthropod activity was accounted for, but in 1971 and 1972 the entire season (May to early September) was included.

I used plastic dishes (diam. 95 mm), plastic cups (diam. 61 mm) and tins (diam. 73 mm), though one type only at any given site. I subjectively placed all traps in

representative patches of the three basic micro-habitats: 1) gravelly bare surface, 2) mesic mossy hollow, 3) *D. octopetala* mat cover. The largest number of traps at any one community was 13 in stand 3 (Table 15) in 1970 and 1971. Emplacement was flush with the soil surface. Blowing sand or organic debris clogging the traps was not a serious problem. The traps were half-filled with a 40-50% solution of ethylene glycol (1970) or commercial antifreeze (1971-2) together with a few drops of formalin and liquid detergent (cf. Leech 1966).

Servicing was at ca. 2-week intervals except in 1972 when I could only manage it once a month. All organisms were transferred to vials with 70% ethyl alcohol, sorted into major groups in the field-lab, then sorted in detail and counted at the University of Alberta. Many specimens were sent to experts for identification, mainly at the Biosystematics Research Institute, Agriculture Canada, Ottawa. Adult Coleoptera were mounted on pins or points. Hymenoptera and Diptera larger than ca. 3 mm were mounted on pins or points using basically the ethyl acetate/glycerol method described by Vockeroth (1966). The rest were sent in 70-75% ethyl alcohol.

5. Pitfall trapping was used to compare the arthropod fauna of *Dryas* tundra with that of other community types. I selected forb meadow, heath tundra and snowbed sites and put in a few traps (Table 32).

6. Other collecting methods were used to augment

the pitfall-trap data:

i. Hand collecting. This met with only limited success and was abandoned except in *Dryas* phytophage studies and random collecting of some arthropods that I happened to spot. Schmoller (1971), studying alpine tundra arthropods in Colorado, found hand collecting and sweeping rather unproductive.

ii. Sun-funnel extraction. I set up Berlese extraction equipment outdoors near camp, and tested it with some litter samples. On clear days the heat of the sun drove arthropods through, but on overcast, cool days the equipment appeared very inefficient.

iii. Tullgren funnel extraction. On 20 Sept 1971 I collected twenty 25x25 cm surface samples at random intervals (1-10 m) along a transect across a terracette *Dryas octopetala*/lichen community (stand 3, Table 15). I collected other surface samples from various microsites mainly in *Dryas*-dominated vegetation, at different times of year including winter. The samples were transported to Edmonton, inverted onto wire mesh, and arthropods extracted into 70% alcohol by use of 4 dm diam. Berlese funnels with 25-watt bulbs. Minimum extraction time was three days.

Edwards and Fletcher (1971) studied a variety of extraction techniques and found that the Tullgren method, the most popular with entomologists, yielded higher numbers of arthropods than most other methods. The Macfadyen air-conditioned, high-gradient method was the most efficient,

yielding 1½-2 times as many mites and collembolans of most groups as the Tullgren method.

DRYAS-VERTEBRATE INTERACTION IN THE BALD HILLS

White-tailed ptarmigan and horned larks breed in upland tundra, usually *Dryas octopetala*/lichen communities. Gray-crowned rosy finches nest in cliffs and forage through all sites with prostrate or sparse vegetation. The only mammals in the area that can be identified with *Dryas* tundra are the golden-mantled ground squirrel, least chipmunk, pika and Rocky Mountain caribou. The rodents prefer irregular rocky terrain. The pika occupies boulder fields and coarse talus. The caribou's common occurrence in winter on *Dryas* tundra, where it paws for lichens, is related to the very thin snow-cover here. None of the four are restricted to upland tundra or indeed the alpine zone.

The carnivores in the area are very wide ranging and cannot be slotted into any specific tundra habitat. A large variety of other birds and mammals, accidentals and migrants, have been spotted in *Dryas* and other communities (Appendix 3).

D. octopetala seems virtually untouched by tundra mammals. I sometimes noted upper portions of *Dryas* leaves nipped off. This was probably accidental, by caribou concentrating on lichens. I once saw chipmunks collecting *D. octopetala* seeds, but this was the only observed instance of utilization. Chipmunks are very scarce in the study area.

The golden-mantled ground squirrel might likewise collect *Dryas* seeds but I have no proof of this. Although pikas occupy rocky slopes that may have much *D. octopetala*, they seem to ignore it. Examination of several haypiles revealed a wide selection of vascular plant species, but no *Dryas*. Martin et al. (1951) reported 2-5% utilization of *Dryas* by west coast pikas. Other studies of pikas do not mention *Dryas* (Sharp 1973).

Of the birds, all but the ptarmigan can be easily dismissed. The pipit has an exclusively animal diet (Verbeek 1970), and rarely frequents *Dryas* tundra. *Dryas* seeds have not been recorded in crop contents of rosy finches or horned larks (Martin et al. 1951). By consuming seeds of the other plant species, these birds could conceivably be decreasing competitive pressure on *Dryas*. Their effect on invertebrate populations in the Bald Hills, and the significance of this with respect to *D. octopetala*, cannot now be answered.

I have no conclusive evidence that white-tailed ptarmigan utilize *D. octopetala* in the Bald Hills. During the winter, when it is the chief exposed vascular plant on the tundra, the birds feed on willows in subalpine valleys. In early May they concentrate at patches of snow-free tundra and might take *Dryas*, but preferred plant food is becoming available at this time. In July and August ptarmigan inhabit forb meadows and stream-courses which provide greater cover and suitable, abundant food for the chicks. In August the birds

return to upland tundra where they remain until ca. October when snows drive them down.

In east Greenland Gelting (1937) found that utilization of *D. octopetala* leaves by ptarmigan dropped to virtually nil in July and August. They picked some *Dryas* flower buds and blossoms, but the bulk of their food consisted of fruiting parts of various herbaceous species. In the fall, *Salix arctica* was most heavily used. By November the ptarmigan were back to *Dryas* leaves. Studies in Norway (Lid cited in Gelting 1937) revealed a similar cycle of *Dryas*-forbs-*Dryas* utilization.

From mid-September to late May, *Salix* provides 90% of the diet of ptarmigan in Colorado (May and Braun 1972). Some *Dryas octopetala* is taken in winter and spring, a little in fall, but none in summer. Use of *D. octopetala* by ptarmigan in other parts of western N.A. seems to peak in early spring (Weeden 1967). Highest use was seen in two ptarmigan collected in Banff N.P. on 27 May 1958 (Weeden 1967); their crops contained (by weight) 41% leaves and 23% flowers of *D. octopetala*. Spring and fall are the most likely periods in which white-tailed ptarmigan might eat *D. octopetala* in the Bald Hills.

INVERTEBRATE FAUNA IN THE BALD HILLS

Taxonomic groups

Altogether 642 species of invertebrates have been collected in the Bald Hills (Table 33). Large groups are flies, hymenopterans, beetles, spiders and mites. The mite species list (Appendix 2) is incomplete, and moths were also inadequately sampled. Major groups not collected were rotifers, nematodes and enchytraeids. Their inclusion might double the number of species (cf. Mulvey 1963, Ryan 1972, Procter 1973).

Total number of invertebrates collected was ca. 56,000

TABLE 33. Numbers of families, genera and species of arthropods collected in the Bald Hills.

CLASS	ORDER	FAMILIES	GENERA	SPECIES
Crustacea	Calanoida	1	1	1
Diplopoda	Chordeumida	1	1	2
Chilopoda	Lithobiomorpha	1	3	4
Insecta	Collembola	3	12	20
	Ephemeroptera	1	1	1
	Orthoptera	2	2	2
	Plecoptera	2	5	5
	Thysanoptera	1	5	7
	Hemiptera	3	7	8
	Homoptera	5	19	24
	Neuroptera	2	5	5
	Coleoptera	14	42	60
	Trichoptera	1	3	3
	Lepidoptera	9	23	28
	Diptera	30	94	155
	Hymenoptera	21	121	156
Arachnida	Phalangida	1	1	1
	Acarina	38	55	63
	Araneida	12	55	97

in pitfall traps, 50,000 in Tullgren extraction samples, and a few hundred hand-collected. Most plentiful in the pitfall samples were flies (48%) especially Sciaridae, Phoridae and Anthomyiidae, large mites (19%) especially Trombidiidae and Erythraeidae, and collembolans (18%). Mites formed the bulk of the extraction samples, which best reflected the arthropod fauna of given microsites. Their major drawback was the large time expenditure yet low yield of most arthropods except mites. Pitfall sampling was much more practical for evaluating patterns of seasonal and spatial distribution of macro-arthropods. This method too has drawbacks: catch numbers reflect mobility rather than population size. They may also reflect the positive or negative response of a given species to the trap, or the variability of this response under different conditions of plant cover and microrelief. There are also strictly mechanical problems, particularly those of trapping fluid evaporating or the trap filling with sand or organic debris. Southwood (1966) has discussed problems in pitfall trapping.

The most conspicuous arthropods on the tundra were flies, especially anthomyiids. The large anthomyiid *Quadrularia laetifica* seemed ubiquitous. March flies (*Bibio*), in August exceedingly abundant on mesic tundra, created a background hum on mild days with little wind. Syrphids were common around flowers. *Metasyrphus lapponicus* abounded in *Abies* thickets along with smaller numbers of wasps (mostly *Vespula norvegicoides*) which it possibly mimicked. Biting flies included mosquitoes (*Aedes* spp.), no-see-ums

(Ceratopogonidae), horseflies (*Hybomitra* spp.) and blackflies (Simuliidae). None were present in large numbers, and were not bothersome except on the rare days of very light wind. MacLean and Pitelka (1971) reported very prominent insect activity, mainly flies, on tundra near Barrow, Alaska. Whereas the fly swarms there were heavily preyed upon by birds especially shorebirds, predator pressure in the Bald Hills seemed low.

Other readily apparent arthropods were bumblebees (*Bombus*) and wolf spiders (Lycosidae). The noctuid *Anarta melanopa* was commonly seen in rocky areas. Butterflies, especially *Nymphalis milberti*, were abundant in flowery meadows though rare elsewhere.

Although the preceding arthropod groups provided most of the visual records of insect activity in the Bald Hills tundra, they were far outnumbered by mites especially oribatids. These were ubiquitous and, together with collembolans, formed the numerical bulk of the arthropod fauna (Tables 34,35).

Ecological groups

Viewed functionally, the Bald Hills arthropod fauna includes five major groups:

1. Phytophages. These include Homoptera, Hemiptera, and larvae of Lepidoptera and some Diptera (leaf-miners) and Hymenoptera (sawflies). Here as in other tundra areas they are not nearly so important, in species richness or population numbers, as in temperate and tropical ecosystems.

TABLE 34. Major plant and arthropod components of 25x25 cm extraction samples collected in the vicinity of the Bald Hills fire lookout, 20 Sept 1970. Animals as no/.1 m^2.

PLANT COVER	*D. octopetala* (W aspect)		*Dryas octopetala/ Polytrichum piliferum*						*Empetrum nigrum* mat				*Phyllodoce glanduliflora*	*Lepraria neglecta*		*Polytrichum juniperinum*
SAMPLE NO.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
VASCULAR PLANT COVER	15	25	25	9	8	5	1	0	80	75	75	75	60	6	6	12
BRYOPHYTE COVER	3	+	1	1	1	60	20	0	2	5	10	5	1	4	2	90
LICHEN COVER	12	2	12	20	10	10	30	0	2	5	+	5	5	50	55	3
INSECTS	24	10	16	6	18	10	11	2	3	8	10	14	22	31	16	51
Chorizococcus sp.	11	5	13		16			2	3					2		
others	13	5	3	6	2	10	11			8	10	14	22	29	16	51
COLLEMBOLA	276	18	24	53	10	87	125	6	8	21	6	73	79	270	219	212
Entomobrya nivalis	5	3	6	8					3	19		67	3	2		5
Folsomia quadrioculata	22			26	2	13	88			2	2		70	198	205	181
Isotoma spp.	70	2	16	19	6	74	37	6	5		3	6	6	70	14	2
Tomocerus flavescens			2		2	3										
others	179	13		2							2					24
SPIDERS	2	2	3	2	2	2	5		3	13	11	10	5	10	14	11
MITES	1813	1231	1291	1037	687	1290	1324	344	317	539	798	751	2303	5684	5455	1442
Mesostigmata	85	27	6	11	5	34	38		6	19	126	10	40	11	38	34
Prostigmata	515	282	363	466	426	62	59	253	29	30	118	50	141	67	83	192
Oribatei	1213	922	922	560	256	1194	1227	91	282	490	554	691	2122	5606	5334	1216
TOTAL NO. ARTHROPODS	2115	1261	1334	1098	717	1389	1465	352	331	581	825	848	2409	5995	5704	1716

NOTE: Sample no. 6 had high bryophyte cover.
Sample no. 7 had high lichen cover.
Sample no. 8: shale-pebble surface.

+<0.5% cover.

TABLE 35. Major plant and arthropod constituents of extraction samples collected on 11 Nov 1970. Animals as no./m^2.

SAMPLE NO.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Elevation (m x 100)	226	226	226	226	226	228	228	228	221	221	217	214	222	222	214	225
Aspect & deg. slope	N3	N3	N3	N3	N3	S2	S2	S2	SW10	SW10	W25	S25	0	0	N4	SE1
Sample area (cm^2)	625	625	690	250	625	255	240	160	60	60	110	200	220	210	300	200
Sample volume (cm^3)	3125	1550	2200	3200	3750	750	850	-	-	200	380	1600	1100	1680	2100	150
COVER TYPE																
Dryas octopetala/lichen community																
bare gravel surface	x	x														
D. octopetala surface			x	x	x											
Kobresia bellardii community						x	x									
D. octopetala mat in above.								x								
Potentilla nivea cushion									x	x						
D. octopetala mat on steep W aspect											x					
Arctostaphylos uva-ursi mat												x				
Artemisia norvegica/Salix arctica community													x	x		
D. octopetala mat in above															x	
Eriophorum/Calliergon community																x
INSECTS	16	32	218	1200	768	274	626	375	667	1000	1464	850	7235	2761	1032	200
Chorizococcus sp.	16	32	189	1120	736	118		188				1100			133	
others			29	80	32	157	626	188	667	1000	364	850	7235	2761	899	200
COLLEMBOLA	16	352	551	1760	640	3567	6589	2000	333	500	2182	2000	6870	666	2664	0
SPIDERS	0	0	87	0	32	118	292	125	0	0	0	100	136	571	133	0
MITES	1712	1472	27057	13720	25696	36691	29732	17938	8335	18504	19361	44600	15334	9092	26074	48850
Mesostigmata	0	0	769	320	32	784	459	313	1501	167	636	850	1092	286	633	0
Prostigmata	1360	448	8178	1440	7168	22893	14970	7250	4167	3667	3545	25900	5597	2380	6260	0
Oribatei	352	1024	18111	11960	18496	13014	14303	10375	2667	14670	15180	17850	8645	6426	19181	48850
TOTAL NO. ARTHROPODS	1744	1856	27913	16680	27136	40650	37238	20438	9335	20004	23007	48650	29575	12662	29903	49050

2. Pollinators. Strictly speaking phytophages, but obtaining a special type of food, these are headed up by many flies together with bumblebees, moths and butterflies.

3. Scavengers & detritus feeders. This is the largest group, with ca. 200-250 species. Many beetles, collembolans, fly larvae and mites obtain their nutrition from organic debris.

4. Carnivores. Included is 20% of the fauna. All spiders are carnivorous, as are some mites and a few insects.

5. Parasites. Comprising 25% of the fauna, this group is headed up by many Hymenoptera, especially ichneumonids. Also parasitic are some flies (Tachinidae) and the immature stages of some mites.

Alpine tundra fauna

Probably 80-90% of the species listed in Appendix 2 are a legitimate part of the tundra fauna, completing their life cycles here. The rest are accidentals, flying in or blown in from subalpine ecosystems. There are many references in the literature to summit-frequenting insects (e.g. Caudell 1902, Chapman 1954a),and masses of insects blown onto snowfields and glaciers (e.g. Van Dyke 1919, Edwards 1972). Insect "fallout" on such a scale was not seen in the Bald Hills. A thin smattering of Homoptera on snowfields in spring was the furthest extent to which this phenomenon manifested itself.

Approximately 15% of the Bald Hills arthropod species are undescribed. The life histories of most of the others have not yet been worked out.

ARTHROPOD INTERACTION WITH *DRYAS OCTOPETALA* FLOWERS

Flies seemed the commonest visitants of *D. octopetala* flowers. In the Bald Hills are members of many of the fly genera and families reported from *Dryas integrifolia* flowers in the High Arctic (Kevan 1970), and it is reasonable to infer that they behave similarly here. Fourteen specimens were collected on *D. octopetala* flowers: 2 of *Megaselia* (Phoridae), 3 *Platycheirus* (Syrphidae), 2 *Rhamphomyia*, (Empididae), 2 *Phaonia*, 2 *Hylemya*, and 3 *Lasiops* (Anthomyiidae). Anthomyiids seemed to be the commonest types at the flowers. Tiny dark humpbacked flies (Phoridae), genus *Megaselia*, were also common and very active, entering the flowers and walking on the hypanthial segment exposed between stamen bases and ovary.

Pitfall data do not offer strong evidence that *Dryas* is important for flies in the study area. Many more flies of most kinds were collected in forb meadows and cushion-rosette tundra than in *Dryas* tundra (Table 36). Furthermore, the seasonal abundance of flies in the Bald Hills did not seem to coincide with *Dryas*' flowering peak (Tables 37,38), i.e. mid June - early July. The best correlation between fly and flowering peak was with *Megaselia* spp. and Anthomyiidae in 1972 (Table 38). Both showed a bimodal pattern, the early peak probably signifying flower-correlated fly activity in *Dryas*

TABLE 36. Mean numbers of flies belonging to the most important *Dryas*-visitant groups, collected in pitfall traps in different plant communities in 1971 and 1972. Values adjusted to represent the average microsite in each community.

FLY GROUP	PLANT COMMUNITY	YEAR	28 May- 15 June	15 June- 11 July	11 July - 9 Aug	9 Aug- 9 Sept	9 Sept- 10 Oct
Megaselia	forb meadow	1971		2.3	43.3	47.3	0.3
	heath	1972		0.8	2.8	6.4	0 ?
	Dryas/lichen	1971	2.2	3.5	4.2	1.2	0.1
	"	1972		14.3	13.6	10.1	
	Dryas/lichen (conglomerate)	1972		2.3	6.5	12.3	
	cushion-rosette	1971			0.3	1.0	
	"	1972		1.0	1.4	1.5	
Anthomyiidae	forb meadow	1971	0	0.7	16.3	26.7	0
	heath	1972		0.8	6.3	2.5	0
	Dryas/lichen	1971	1.4	4.7	7.7	2.3	0.4
	"	1972		6.8	5.4	10.8	
	Dryas/lichen (conglomerate)	1972		5.7	10.5	4.5	
	cushion-rosette	1971			7.7	51.0	
	"	1972		0	30.3	4.5	
Empididae	forb meadow	1971		0	0	2.7	3.0
	heath	1972		0.2	0.3	1.4	0 ?
	Dryas/lichen	1971	0.2	0	0.6	0.1	0
	"	1972		0	2.8	3.5	0
	Dryas/lichen (conglomerate)	1972		0	0	0.8	
	cushion-rosette	1971			0	0.3	
	"	1972		0	0	0	
others (except *Bradysia*)	forb meadow	1971		8.7	18.3	40.3	4.7
	heath	1972		0.2	10.5	2.2	0 ?
	Dryas/lichen	1971	1.3	2.0	1.5	1.8	0.8
	"	1972		3.3	5.1	2.8	0
	Dryas/lichen (conglomerate)	1972		3.0	4.8	1.6	
	cushion-rosette	1971			5.3	16.7	
	"	1972		0	20.7	2.5	

TABLE 37. Numbers of arthropods caught in pitfall traps in the Bald Hills through the 1971 season.

SAMPLING PERIOD	28 May- 15(20)June	15(20)June- 11 July	11 July- 7 Aug	7 Aug- 7 Sept	7 Sept- 10 Oct	TOTAL
NO. TRAPS	22	23	25	25	24	29
DIPLOPODA			12	34	8	54
CHILOPODA		2	3	1	1	7
COLLEMBOLA						
Sminthuridae	3	30				33
Entomobrya nivalis	216	34	1100	61	6	1417
Isotoma spp.	262	240	395	135	95	1027
Morulina nr. *gigantea*	84	19	36	26	4	169
Tomocerus flavescens	57	24	107	103	32	313
HOMOPTERA						
Empoasca sp.			115	146	2	263
Scleroracus sp.	1		9	31	4	45
Psylla americana	4	8	1	25	1	39
Trioza sp.	2	8	1			11
Aphididae	2		2	4		8
Pseudococcidae	3	2		2		6
COLEOPTERA						
Carabus taedatus	8	9	2			19
Nebria intermedia	4	2	12	8	2	28
Arpedium brunnescens			27		2	29
Mycetoporus n.sp.	2		3	9	3	17
other Staphylinidae	1		6	6		13
Cantharidae	1		7	7	9	24
Byrrhus spp.	4	11	7	3	1	26
others	4	2	33	36	3	78
NEUROPTERA		5				5
LEPIDOPTERA						
Rhopalocera ad.		8	3			11
lar.		4	1			5
Noctuidae ad.	10		10	5		25
lar.	5	11	37	10	2	65
Nepticula spp.	173	109	5			287
others	7		7	1		15
DIPTERA						
Bradysia spp.	12	126	694	1968	20	3376
Megaselia spp.	31	43	276	170	2	527
Mycetophilidae	2	25	47	10		84
Empididae	2		18	13		33
Anthomyiidae	23	73	440	110	4	650
Tachinidae		33	51	10	2	96
others	21	36	122	152	23	354
HYMENOPTERA						
Tenthredinidae	4	4	9	4	4	25
Braconidae	12	17	30	24	1	84
Ichneumonidae	9	14	35	132	15	205
Chalcidoidea	21	1	9	40		71
Proctotrupoidea	7		18	40	1	68
Bombus spp.	26	34	22	92		174
PHALANGIDA			6	10		16
ACARINA						
Abrolophus sp.	1	8	55	11		75
Erythraeus sp.	36	326	1314	197	7	1880
Podothrombium malignum	56	88	1679	643	88	2554
Microtrombidium sp.	42	43	58	158		434
Parasitoidea	64	33	3	15	1	116
ARANEIDA						
Arctosa insignita	10	1	14	2	-	27
Argenna lorna	2	14	27	3	-	46
Ceratinopsis labradorensis	31		4	7	-	42
Gnaphosa spp.	2	2	14	6	-	24
Hahnia glacialis			21	20	-	41
Pardosa furcifera	4	11	45	6	-	66
other *Pardosa* spp.	2	12	72	16	-	94
Rhaebothorax n.sp.	26	10	28	125	-	189
Typhochraestus pygmaeus	53	2	9	62	-	126
Xysticus spp.	6	10	27	12	-	54
other Linyphiidae	14		35	82	-	130
others	12	17	30	9	-	68

TABLE 38. Numbers of arthropods caught in pitfall traps in the Bald Hills through the 1972 season.

	before 11 June	11 June-11 July	11-27 July	27 July-11 Aug	11 Aug-10 Sept	TOTAL
DIPLOPODA			2	6	8	16
COLLEMBOLA						
Sminthuridae	3		16	1		20
Entomobrya nivalis	318	208	751	535	170	1982
Isotoma spp.	304	384	604	589	406	2287
Morulina nr. *gigantea*	18	49	47	142	157	413
Tomocerus flavescens	18	46	144	118	221	547
HOMOPTERA						
Empoasca sp.				4	129	133
Aphididae			1	2	2	5
Pseudococcidae	3	33	5	2	4	47
others	6	8	6		8	28
COLEOPTERA						
Carabus taedatus			3	13	8	24
Nebria intermedia		2	7	6	16	31
Staphylinidae	14	7	7	7	8	43
Cantharidae		2	2	9	22	35
others	6	5	9	12	35	67
LEPIDOPTERA						
Noctuidae ad.		1		5	8	14
lar.	6	28	53	36	15	138
Nepticula spp.	5	84	3	2		94
others	4		6	3	1	14
DIPTERA						
Bradysia spp.	5	45	483	3098	9095	12726
Megaselia spp.	14	426	109	95	210	854
Mycetophilidae	1	3	2	12	8	26
Empididae		1	7	22	35	65
Anthomyiidae	4	103	84	158	150	499
Tachinidae	1	1	31	19	22	74
others	25?	42	105	60	27	259
HYMENOPTERA						
Tenthredinidae	2	1	8	5	7	23
Braconidae	3	10	18	11	21	63
Gelis spp.		8	12	18	23	61
Other Ichneumonidae	4	11	38	100	287	440
Chalcidoidea	31	9	39	69	44	192
Proctotrupoidea		1	3	26	24	54
Bombus spp.	15	49	30	7	33	134
ACARINA						
Erythraeus sp.	28	106	182	179	275	770
Podothrombium malignum	35	142	178	675	1058	2088
Microtrombidium sp.		94	132	45	29	300
Parasitoidea	49	72	20	3	1	145
ARANEA	-	336	306	391	300	1361

communities. Peak numbers of flies in *Dryas*/lichen tundra later in the season (Table 36) probably represent an influx from forb meadows and forest-tundra habitats.

As in the High Arctic (Kevan 1970), bumblebees and Lepidoptera were the two other important pollinator groups. The common moth *Anarta melanopa* was occasionally seen at *D. octopetala* flowers. Adults of leaf-mining microlepidoptera in the genus *Nepticula* were often seen at *D. octopetala* flowers. All 380 pitfall-trapped specimens were from *Dryas* tundra. *Nepticula* activity peaked early in the season (Tables 37,38), more or less coincident with *Dryas* flowering. Most moth and butterfly activity in the Bald Hills was in late July and August at forb meadows, especially where *Senecio triangularis* and *Arnica mollis* were abundant.

Five species of bumblebees (*Bombus*) foraged in the Bald Hills. Largest numbers were seen and trapped in forb meadows (Table 39), but some were trapped in various xeric communities. Peak catches were late in the season in 1970 and 1971 but early in the season in 1972 (Tables 37,38, Appendix 10). Bumblebees were seen at *Dryas* flowers in only three of 135 recorded observations. Early in the season they were attracted to staminate aments of *Salix arctica*. In mid-season they visited a wide variety of species, but with an evident bias toward *Pedicularis arctica*. Later in the season *Arnica mollis* and *Senecio triangularis* were heavily used. Gavriliuk (1961), however, considered bumblebees very important *Dryas* pollinators in Chukotk.

Four noctuid larvae were collected from *D. octopetala* flowers. One was *Zosteropoda hirtipes*, by far the commonest

TABLE 39. Average numbers of arthropods per trap caught in pitfall traps in the 1971 season in different microhabitats.

COMMUNITY	*Dryas octopetala*/lichen (2250 m)				*D. octopetala*/lichen (2590 m)		*Cassiope tetragona*/ *D. octopetala* (2530 m)	*Artemisia norvegica*/ *Salix arctica* (2225 m)	cushion-rosette (2320 m)
	Dryas mat	bare shale	hollow	*Empetrum* mat	*Dryas* mat	gravel			
SAMPLING PERIOD	28 May-10 Oct				5 June-8 Oct		5 June-8 Oct	11 July-10 Oct	11 July-7 Aug
DIPLOPODA							11.3		
CHILOPODA	0.8	0.8							
COLLEMBOLA									
Sminthuridae		10.3				0.7			
Entomobrya nivalis	17.7	61.5	6.0	9.0	8.8	16.7	9.0	3.5	341.3
Isotoma spp.	31.0	21.6	90.5	37.5	40.6	76.8	52.8	6.5	55.7
Morulina nr. *gigantea*	10.1	0.3	15.5	0.5				14.5	
Tomocerus flavescens	10.5	3.0	9.0	4.0	7.8	1.0	93.5	31.0	
HOMOPTERA									
Empoasca sp.							0.8	43.0	
Soleroranus sp.		0.3		0.5				10.5	
Psylla americana	0.5	1.8	0.5	0.5		0.3	0.3	2.0	
COLEOPTERA									
Carabidae	3.3	1.6	1.0	0.5				14.0	0.7
Staphylinidae	2.1	2.6		1.5			0.8	30.0	1.3
others	4.0	5.9	3.0	1.0	4.3	1.6	0.9	4.0	0.7
LEPIDOPTERA									
Noctuidae ad.	1.7		0.5		0.5	0.3	2.1	0.5	0.7
lar.	0.8	0.3			1.8	12.4	2.0	1.0	8.0
Nepticula spp.	22.9	27.3	10.0	22.0		0.3	1.8		
DIPTERA									
Bradysia spp.	411.3	191.2	150.0	90.0	16.7	8.5	17.9	29.0	24.0
Megaselia spp.	8.6	15.6	15.0	12.0	1.1	0.8	8.1	51.0	1.3
Anthomyiidae	16.5	18.6	16.0	12.0	3.0	9.2	8.1	33.5	58.7
others	9.3	12.5	6.5	1.0	17.4	22.9	12.9	61.0	22.3
HYMENOPTERA									
Tenthredinidae	1.5	1.2	0.5	0.5	0.3	1.2	1.4		1.0
Braconidae	5.5	2.5			2.3	1.5	3.6	6.5	3.3
Ichneumonidae	10.8	10.9	0.5	4.0	2.0	6.5	8.6	15.5	0.7
Chalcidoidea	4.6	1.6	1.5	2.0	0.8	1.6	1.5	6.5	
Proctotrupoidea	1.0		1.5					15.5	
Bombus spp.	8.1	12.7	4.0	2.0	2.3	3.8	2.5	18.5	3.3
PHALANGIDA					0.3	6.5	1.3		
ACARINA									
Abrolophus sp.	0.7	2.0	1.5	1.5	3.0	2.2	0.7		14.7
Erythraeus sp.	166.5	54.9	264.5	93.5				1.5	
Podothrombium malignum	132.3	50.2	372.0	100.5	360.7	136.3	15.3	158.5	8.0
Microtrombidium sp.	14.9	3.4	7.5	3.0	6.0	64.7	7.0	4.0	
Parasitoidea	5.3	14.0	7.0	2.5	0.3	0.3	5.8		
ARANEA									
Pardosa spp.	0.3	0.5	0.5	0.5	2.3	1.9	9.6	36.0	0.3
Linyphiidae	24.0	42.6	30.3	9.1	0.9	3.6	13.6	25.0	11.7
Xysticus labradorensis	5.2	2.5	1.5	1.0	1.3	2.3			
others	3.8	2.2	9.0	5.5	0.9	1.9	21.4	4.5	

lepidopterous larva in the Bald Hills; the others could not be identified. On 21 June 1971 I collected 175 *D. octopetala* flowers in a S-facing *Dryas*/lichen community. Six had frass on the hypanthium, evidence of larval activity. Only one had a caterpillar. Other observations corroborate this evidence for a very low incidence of attack by lepidopterous larvae. Noctuid larvae can be fairly abundant in upland tundra but do not seem to attack *Dryas* much. In other parts of the Rockies I have seen *D. octopetala* flowers with their floral parts, usually the gynoecium but sometimes part of the androecium, eaten away, probably by moth larvae.

Also seen at *D. octopetala* flowers in the Bald Hills were a few crab spiders (*Xysticus labradorensis*). These lurked within the floral cup, ambushing flies attracted to the blooms. This is the same phenomenon that Leech (1966) reported for *X. deichmanni* at *D. integrifolia* flowers in the High Arctic. Some arthropods probably use the flowers simply as perching sites. Groups of plants in flower might be used as swarm markers by certain flies (Kevan 1970).

Heliotropism of *Dryas integrifolia* flowers in the Arctic results in floral-cup temperatures well above ambient (Kevan 1970). This is advantageous to insects, for they can achieve a higher metabolic rate than in normal tundra environments. From photographs taken at different times of day at five marked *D. octopetala* mats in the Bald Hills, I saw possible evidence of heliotropism in only one case, and this involved flowers with longer-than-normal scapes. Flower

orientation appeared a function of position on the mat, with edge flowers normally facing outward. Since there were generally more flowers along the south edges of mats, a second-order heliotropism obtained.

Dryas can set seed autogamously, though seed set is enhanced by pollinator activity (Kevan 1970). *Dryas* reproduction in the Bald Hills seems mostly vegetative, so pollinators are probably not important in its success here.

HERBIVORES OF *DRYAS OCTOPETALA*

Aside from nectar and pollen feeders, I found only two species of arthropods dependent on *D. octopetala* as the major and probably sole food source. These were a mite, *Eotetranychus* sp. (*tiliarum* grp.) and a mealybug, *Chorizococcus* sp. One aphid (*Acyrthosiphon* sp.) and one or more noctuid larvae may be at least partly reliant on *D. octopetala* for food.

Eotetranychus sp.

Eotetranychus sp. is a small red spider mite inhabiting the leaf undersides of *D. octopetala*. It prefers young but at least partly expanded leaves, and rarely occurs on any other part of the plant. Some clones seem free of the mite, but most are infested. The one mat I examined in detail had 82 fascicles and 323 leaves, inhabited by 131 mites. There were 93 mites on fully expanded leaves (0.57 mites/leaf), 38 mites on partly expanded leaves (0.36 mites/leaf), and none

on the 54 tiny inrolled leaves. There was an average of 1.70 mites per occupied leaf, six being the largest number on one leaf. All but six mites were on the leaf underside.

The mite occurred in all extraction samples from *Dryas*-dominated tundra, but in none of the samples from tundra lacking *Dryas*. Thus, it occurred in only sample nos. 1-5 in Table 34). The numbers of adults (all females) were, respectively, 51, 64, 269, 266 and 35. Wide fluctuation in numbers from sample to sample was also seen in other extraction samples from *Dryas* tundra. No correlation was apparent between numbers of these mites and percent cover of *D. octopetala* (Fig. 28).

Eotetranychus sp. was found in all *Dryas*-mat extraction samples, even those isolated in other vegetation (e.g. Table 35, sample no. 15 in a forb meadow and no. 8 in a *Kobresia* community). Wind or phoresy are probably involved in transportation to these "island" sites.

Populations of *Eotetranychus* sp., as reflected by extraction samples, were largest in midwinter and lowest in fall (Table 40). Very high midwinter numbers of *Eotetranychus* (equivalent to 10000/m^2) were found in *D. octopetala* mats on a W-facing slope (Table 41). In late April, exposed *D. octopetala* mats had much higher mite densities than snow-covered ones (Table 42).

Eotetranychus sp. seems to stay on *D. octopetala* leaves most or all year. It overwinters on the leaves in both adult and immature stages, and might even be active whenever

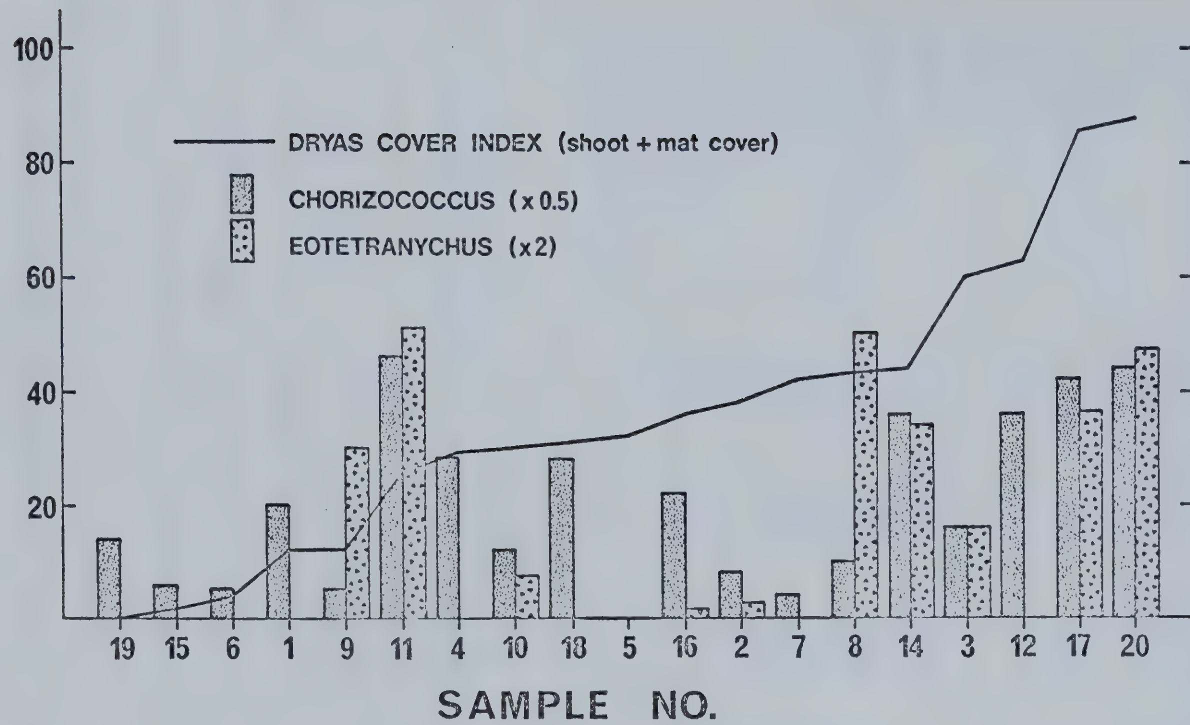

FIG. 28. Relationship of *Dryas octopetala* cover to numbers of *Chorizococcus* sp. and *Eotetranychus* sp. (adult females) in a *D. octopetala*/lichen community (stand 3). Extraction samples (625 cm^2 each) collected 20 Sept 1970.

TABLE 40. Mean numbers of arthropods in extraction samples of *Dryas octopetala* mats from a *D. octopetala*/lichen community (stand 3), sampled at different times of year. Animals as no/.1 m^2.

DATE	1970		1971		
	20 Sept	11 Nov	27 Feb	25 Apr	11 July
INSECTS					
Chorizococcus sp.	30	68	29	5	20
others	4	5	0	1	150
COLLEMBOLA	112	98	4	20	225
SPIDERS	7	4	1	1	0
MITES	2318	2216	2305	850	2950
Mesostigmata	34	37	7	12	40
Prostigmata	567	560	264	142	415
Eotetranychus sp.[a]	94	159	174	88	90
others	473	401	90	54	325
Oribatei	1717	1619	2034	696	2495
grp.1[b]	244	194	400	215	180
grp.2	1473	1425	1634	481	2315
ALL ARTHROPODS	2471	2391	2339	877	3345

[a]Adult females.

[b]Cf. footnote p.253.

leaf temperature exceeds a certain threshold.

Some of the samples of *D. octopetala* leaves, e.g. 27 Feb 1971, had small numbers of a prostigmatid mite (*Abrolophus*?). This mite might be a predator of *Eotetranychus* sp. The densities of the predator, ca. 100-400/m^2 in *D. octopetala* cover, were 10-50 times fewer than the numbers of *Eotetranychus*.

Chorizococcus sp.

The mealybug *Chorizococcus* sp. has close taxonomic affinities with an arctic *Dryas* feeder, *C. altoarcticus* (W.R. Richards, *pers. comm.*). It was collected in both pitfall and

TABLE 41. Arthropod components of extraction samples of tundra surface samples collected 27 Feb 1971. Animals as no/.1 m^2.

SAMPLE	1	2	3[a]	4	5	6	7	8
ELEVATION (m)	2260	2260	2190	2190	2230	2230	2230	2230
ASPECT & DEG. SLOPE	N3	N3	W20	W20	W15	W15	W15	W15
SAMPLE AREA (cm^2)	400	400	400	400	180	63	70	100
PLANT COVER								
Dryas octopetala mat	x	x	x	x				
Potentilla nivea cushion					x	x		
Silene acaulis cushion							x	x
INSECTS	33	25	8	5	228	0	29	10
COLLEMBOLA	3	5	0	0	0	0	286	130
SPIDERS	0	3	0	0	0	0	0	0
MITES	2193	2416	1453	1083	1200	746	2929	930
Mesostigmata	5	8	0	0	22	0	143	60
Prostigmata	175	353	1425	928	473	0	1243	290
Eotetranychus sp.[b]	133	215	1010	860	0	0	0	0
others	42	138	415	68	473	0	1243	290
Oribatei	2013	2055	28	155	705	746	1543	580
grp.1	260	540	10	90	11	48	143	0
grp.2	1753	1515	18	65	694	698	1400	580
undet. sp.					(4000)	(950)		
ALL ARTHROPODS	2229	2449	1461	1088	1428	746	3244	1070

[a]Only live *D. octopetala* leaves and stems.
[b]Adult females.
[c]Cf. footnote, p.253.

extraction samples. Its numbers were smaller but less extreme in contagion (Table 43) than those of *Eotetranychus* sp.

Although doubtless dependent on *D. octopetala* for food, *Chorizococcus* sp. was not as intimately correlated with its host as was *Eotetranychus*. It was evidently more mobile. Small numbers were consistently collected on bare gravel patches in *D. octopetala*/lichen communities (e.g. Table 35, sample nos. 1 & 2), and even in non-*Dryas* plant cover (Table

TABLE 42. Arthropod components of 15 cm^2 extraction samples of tundra surface collected 25 April 1971 in a *Dryas octopetala*/lichen community (stand 3). Animals as no/.1 m^2.

SAMPLE NO.	bare pebbles	*Dryas* mat cover				
	1	2[a]	3	4	5	6
snow depth (cm)	0	0	0	0	30	40
cryptogram cover	+	25	30	45	20	15
INSECTS						
Chorizococcus sp.	1	2	3	1	8	9
others	0	2	0	1	0	0
COLLEMBOLA	5	7	8	79	3	1
SPIDERS	0	0	4	0	0	0
MITES	37	458	1091	975	471	744
Mesostigmata	0	10	14	30	1	5
Prostigmata	8	242	169	208	30	62
Eotetranychus sp.[b]	0	137	114	128	21	41
others	8	105	55	80	9	21
Oribatei	29	206	908	757	440	677
grp.1[c]	7	25	407	130	59	264
grp.2	22	181	501	627	381	413
ALL ARTHROPODS	43	469	1106	1056	482	754

[a]Poor extraction?

[b]Adult females.

[c]Cf. footnote, p.253.

34). Like *Eotetranychus*, it also occurred in *Dryas* mats isolated within foreign vegetation (Table 35). Its activity was, nevertheless, in large part confined to vegetated sections of *Dryas* tundra. It did not occur in vegetation totally lacking *Dryas* (Table 35).

Correlation is poor between *Chorizococcus* population

TABLE 43. Plant and arthropod components of twenty 25x25 cm surface extraction samples collected in a line transect across a *Dryas octopetala*/lichen community (stand no 3) on 20 Sept 1970.

SAMPLE NO.	1	2	3	4	5	6	7	8	9	10	11	12	13*	14	15	16	17	18	19	20	MEAN±ST.E.
VASCULAR PLANT COVER	4	13	17	11	10	2	7	14	7	8	9	22	18	17	1	15	17	9	2	21	11±1
Dryas octopetala																					
mat cover	8	30	45	25	25	3	35	35	8	25	20	50	60	35	1	30	70	25	0	70	26±5
leaf cover	3	8	15	4	7	1	7	8	3	5	5	13	12	9	+	6	15	6	0	18	7±1
others	1	5	2	7	3	1	+	6	4	3	4	9	6	8	1	9	2	3	2	3	4±1
BRYOPHYTE COVER	65	3	6	2	2	+	3	2	10	+	2	2	+	1	+	1	2	20	+	1	6±3
LICHEN COVER	18	25	20	20	15	7	15	10	20	10	25	20	10	30	5	25	15	25	10	15	17±2
TOTAL PLANT COVER	87	41	43	33	27	9	25	26	37	18	36	44	28	48	6	41	34	54	12	37	34±4
INSECTS	10	10	8	15	2	4	3	6	40	6	24	19	3	19	3	16	25	17	7	22	13±2
Chorizococcus sp.	10	4	8	14	0	3	2	5	3	6	23	18	2	18	3	11	21	14	7	22	10±2
others		6		1	2	1	1	1	37		1	1	1	1		5	4	3			3±2
COLLEMBOLA	7	28	118	73	63	142	51	24	228	25	30	39	10	42	13	11	57	63	82	19	56±12
SPIDERS	2	3	7	8	3	0	0	4	2	0	3	7	0	0	0	2	1	1	2	1	2±1
MITES	867	1052	924	1281	785	215	961	1080	1069	556	931	929	218	1071	91	847	786	904	115	857	777±78
Mesostigmata	29	20	35	13	6	0	6	6	19	7	3	24	2	15	0	9	28	8	0	7	12±2
Prostigmata	326	210	149	317	135	33	295	348	211	339	356	122	76	130	28	58	171	37	46	319	185±27
Oribatei	512	822	740	951	644	182	660	726	839	210	572	783	140	926	63	780	587	859	69	531	579±65
TOTAL NO. ARTHROPODS	886	1093	1057	1377	853	361	1015	1114	1339	587	988	994	231	1132	107	876	869	985	206	899	849±81

*Part of sample lost.

numbers and *D. octopetala* cover except possibly near 100% mat cover (Fig. 28).

Like *Eotetranychus* sp., *Chorizococcus* sp. seems to overwinter in all stages including adult. In contrast to *Eotetranychus*, mealybug numbers seemed higher under snowcover than in the open (Table 42). Early winter populations seemed largest (Table 40). Peak activity, however, was in June - early July (Pseudococcidae - Table 38).

Very few mealybugs were trapped in 1971 compared to 1970 and 1972. Year-to-year fluctuation might be due to parasite pressure by *Stemmatosteres kuchari*, a tiny (<1 mm) apterous chalcid. *S. apterus* was reared from a *Pseudococcus* species in California (Yoshimoto 1972). Few collections, and a very irregular temporal and spatial dispersion of *S. kuchari*, obscure the correlation of host/parasite population cycles. The large numbers of *Stemmatosteres* collected later in the 1970 season and early in 1971 might be significant in relation to the low numbers of *Chorizococcus* encountered in 1971.

Other *Dryas* herbivores

Four males of the aphid *Acyrthosiphon* sp. were trapped in meadows, and two nymphs in *D. octopetala* mats. The closely related *A. brevicornis* is a *Dryas* feeder in the arctic (W.R. Richards, *pers. comm.*). *Acyrthosiphon* was evidently not an important *Dryas* phytophage in the Bald Hills during the study period.

Dryas octopetala is host to several species of leaf-mining Lepidoptera in Europe. Examination of literally

thousands of *Dryas* leaves from the Bald Hills revealed only two incidents of mining activity. One involved a species of *Coleophora*, possibly a case of mistaken host identity by the moth. The other entailed a mat under a bit of krummholz in a *Dryas*/lichen community, with a number of the leaves mined.

A low incidence of feeding injury to *D. octopetala* flowers by noctuid larvae has been discussed earlier.

DRYAS OCTOPETALA VEGETATION AND ARTHROPODS

Arthropod fauna

About 330 species of arthropods or 55% of the Bald Hills fauna has been recorded from *Dryas*-dominated tundra. Important groups include mites, collembolans, flies, Hymenoptera and spiders. Many species are quite mobile and easily able to appear in other communities even if they might be dependent on *Dryas*-dominated communities for some part of their development.

Restricted to *Dryas*-dominated communities, or occurring mostly here, are at least 30 species. These include three beetles (*Byrrhus*, *Hyperaspis*, *Podabrus*), two collembolans (*Bourletiella hortensis*, *Folsomia quadrioculata*), five or more flies (*Philigria debilis*, *Bradysia* spp.), at least three parasitic hymenopterans (*Gelis* sp., *Zygota* sp., *Stemmatosteres kuchari*), a few Lepidoptera (*Nepticula* spp., *Argynnis* larvae, certain noctuid larvae especially *Zosteropoda hirtipes*), twelve spiders (*Clubiona praematura*, *Xysticus labradorensis*,

Argenna lorna, Dictyna spp., *Micaria hesperella, Ceratinopsis labradorensis, Cochlembolus alpinus, Cornicularia karpinskii, Oreonetides vaginatus, Rhaebothorax* n.sp., *Typhochraestus pygmaeus*), one bug (*Chorizococcus* sp.), and three mites (*Eotetranychus, Epidamaeus, Gamasellus*). Forty-one species of mites in 22 families have been isolated from *Dryas* tundra in the study area. Some would probably be restricted to this tundra type though not enough specimens were identified to verify this. Many parasitic Hymenoptera, ichneumonids in particular, might find their hosts mostly in *Dryas* tundra, but here again not enough specimens were identified beyond family. Fly adults are very mobile, and it would be difficult to establish community restrictions for most species. An emergence-trap study could delineate larvae-habitat relationships.

Arthropods in pitfall samples

Pitfall traps were effective for most ground-surface arthropods particularly spiders, large mites and collembolans, and beetles. Large numbers of flying insects were caught in the pitfall traps. *Bradysia*, a dark-winged fungus gnat (Sciaridae), outnumbered all others combined. Many other species of flies were caught. Some of the catches may reflect positive response to the ethylene glycol solution. Leaf-miner flies (Agromyzidae) are one group present on the tundra but not caught because, according to G.C.D. Griffiths (*pers. comm.*), they are not attracted to these traps.

Also collected in abundance were the collembolans *Entomobrya nivalis*, *Isotoma viridis*, *I. violacea* and *Tomocerus flavescens*; a variety of spiders, mostly those mentioned above; and the large mite *Podothrombium malignum*. Also trapped at *Dryas* sites were some noctuid larvae, many species but relatively low numbers of ichneumonoids, and few proctotrupoids and chalcids (except *Stemmatosteres*). Very low numbers of beetles and bugs were trapped.

Arthropods in extraction samples

All extraction samples from *Dryas* tundra had overwhelming numbers of mites, amounting to 10000-30000/m^2 at different sites (Tables 34,35,43) and different times of year (Table 40). Oribatids predominated, numerically and in numbers of species. Prostigmatid mites were generally 20-50% as abundant. There were few mesostigmatid mites, mostly *Zercon* spp.

Collembolans formed the only other reasonably abundant group, but not nearly in the numbers expected. Other tundra studies report close to a 1:1 ratio of mites to collembolans (e.g. Bohnsack 1968, Solhöy 1972), but in the Bald Hills mites were ten or more times as numerous. Large losses in *en route* samples might be considered; but the extraction figures likely reflect a real numerical superiority of mites. According to Mani (1962) the mite:collembolan ratio reflects degree of vegetational "maturity". The Bald Hills data would indicate an exceedingly "mature" development! At the very least

they imply a mild environment by tundra standards.

Very low numbers of other organisms, mostly fly larvae, were encountered in extraction samples (Tables 34,35,43). Lateness of the season would partly account for this. But even samples taken in mid-season had relatively low numbers of insects (Table 44). Funnel extraction is obviously far from ideal in studying tundra macro-arthropods. Much destructive sampling and a large expenditure of time and extracting equipment would be necessary to achieve reasonable population estimates.

TABLE 44. Major arthropod constituents of 10x10 cm squares of tundra surface collected 11 July 1971 in a *Dryas octopetala*/lichen community (stand no. 3). Animals as no/.1 m^2.

SAMPLE NO.	1	2	3
PLANT COVER			
Dryas octopetala mat	x	x	
Salix nivalis diffuse mat			x
SPIDERS	0	0	0
COLLEMBOLA	60	390	290
INSECTS			
Chorizococcus sp.	30	10	20
others	230	70	110
MITES			
Mesostigmata	30	50	90
Prostigmata	420	410	580
Oribatei	2410	2580	2380
TOTAL NO. ARTHROPODS	3180	3510	3470

Arthropod activity in different *Dryas* communities

Pitfall catches of *Bradysia* and lepidopterous larvae were higher in *D. octopetala*/lichen than in *D. octopetala*/*Polytrichum piliferum* communities (Table 45). There were no other substantial faunistic differences. Note especially the comparable numbers of mites (Tables 34,43). Relatively few spiders were trapped in the *Artemisia norvegica*/*D. octopetala* community (stand 1, Table 45) which was otherwise quite comparable to *D. octopetala*/lichen tundra. A trap in one *Cassiope tetragona*/*D. octopetala* community (stand 9, Table 45) had fewer spiders, mites and collembolans, but many more Homoptera and beetles than other *Dryas*-dominated communities. The arthropod fauna resembled that of *Phyllodoce*-*Cassiope mertensiana* vegetation.

Traps in a high-elevation *Cassiope tetragona*/*Dryas octopetala* community (Table 39) had more *Tomocerus flavescens* than did those of any other community, but far fewer of most other arthropods. The dense plant cover in this particular community may hamper arthropods' surface activity, resulting in subnormal catches. The numbers of millipedes are one indication of a favorable mesic habitat.

The shale-conglomerate transect (Table 46) brought to light some marked differences in arthropod activity. Higher numbers of all collembolan species except *Tomocerus flavescens* were trapped in the conglomerate section. Also more abundantly trapped here were *Bradysia*, *Megaselia* and Anthomyiidae, along with *Nepticula* adults and noctuid larvae. Other groups

TABLE 45. Mean numbers of arthropods per trap, collected in pitfall traps in the Bald Hills, 1970[1].

	forest-tundra zone, 2135 m								*Dryas octopetala*/lichen stand no. 3, 2260 m			30°E aspect, 2330 m						*Dryas octopetala*/lichen, top of the Bald Hill, 2300 m		25°W aspect, 2200 m			N aspect, 2200 m					
	bare shale	moss & lichen surface[2]	*Lepraria neglecta*	*Dryas octopetala* mat	*Empetrum nigrum* mat	*Phyllodoce glanduliflora*	*Betula glandulosa*	within *Abies lasiocarpa* clone	bare shale	mossy hollow	*Dryas octopetala* mat	*Dryas octopetala* mat	*Cassiope mertensiana*	*Artemisia norvegica-Anemone occidentalis* (stand no. 23, 2230 m)	*Artemisia norvegica-Luzula parviflora* (stand no. 22, 2230 m)	*Artemisia norvegica/Salix arctica* (stand no. 21, 2130 m)	*Carex nigricans* (stand no. 27, 2230 m)	bare shale	*D. octopetala* mat	bare shale	*D. octopetala* mat	*Salix arctica* mat	*Salix arctica* mat	*Luzula* snowbed	*D. octopetala/Artemisia norvegica* (stand no. 1, 2290 m)	*Cassiope tetragona/D. octopetala* (stand no. 9, 2240 m)	*Phyllodoce glanduliflora-Cassiope mertensiana* (2130-2230 m)	*Artemisia norvegica/Phyllodoce-Cassiope* (2220 m)
DIPLOPODA	.	+	.	1	2	2	4	4	.	.	.	1	1	4	9	2	1	.	.	1	14	28	11	8	.	.	1	8
CHILOPODA	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
COLLEMBOLA	53	11	112	30	11	20	30	32	26	35	39	21	90	119	36	59	2	28	37	20	80	107	70	139	38	19	16	28
INSECTA																												
Orthoptera																												
Grylloblatta campodeiformis	.	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	1	.	.	3	1	3	.	1	.	.	.	.
Melanoplus borealis	.	.	.	.	.	.	.	.	.	.	.	.	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Homoptera	8	9	9	6	21	2	9	3	9	4	7	56	42	14	14	33	3	.	2	20	1	5	20	9	2	48	116	30
Coleoptera ad.	5	6	10	7	2	6	12	10	5	14	4	1	9	27	40	25	27	.	.	1	2	3	7	4	4	21	6	77
lar.	.	2	.	3	2	2	6	9	1	2	+	3	5	3	2	3	1	.	.	.	2	2	4	5	1	8	1	.
Lepidoptera ad.	3	3	1	1	7	.	.	.	2	.	1	1	.	.	.	.	.	.	2	.	.	.	.	2	.	.	.	.
lar.	.	3	1	3	2	2	1	1	4	7	5	5	4	2	1	1	.	1	1	.	1	3	.	2	.	2	1	1
Diptera																												
Bradysia spp.	10	18	18	54	10	8	3	11	282	496	297	45	15	41	12	34	3	110	265	7	2	13	1	.	757	1	1	.
others	9	6	19	8	2	4	1	12	9	18	10	40	27	2	1	22	1	4	3	4	9	3	4	6	3	11	2	3
Hymenoptera																												
parasites	6	6	17	4	4	6	7	5	17	2	5	3	6	1	2	8	.	1	2	13	1	3	3	15	5	5	2	2
others	1	5	.	.	4	.	.	1	3	1	1	.	1	2	3	3	1	.	1	1	.	1	.	3	1	.	1	1
PHALANGIDA	.	.	.	.	.	.	.	.	+	.	.	.	1	.	.	.	.	.	.	29	3	.	3	14	.	.	.	.
ACARINA	8	36	410	38	65	21	93	29	18	40	25	-	47	205	-	65	26	6	35	6	38	42	46	5	75	18	48	5
ARANEA	18	23	9	11	9	11	27	22	26	14	15	3	13	38	17	33	9	10	37	5	3	5	7	2	6	7	16	20

[1] Coll. period: 12 July-15 Sept for first 4 grps, 30 July-15 Sept for last 4 grps.

[2] *Polytrichum piliferum, Cetraria* spp., *Cladonia* spp., *Stereocaulon alpinum*.

NOTE: + <0.5

TABLE 46. Numbers of arthropods collected in 1972 in pitfall traps in a transect across *Dryas octopetala*/lichen tundra of two substrate types.

SUBSTRATE & TRAP NO.	SHALE PEBBLE				RISER	CONGLOMERATE			
	115	116	117	118	119	120	121	122	123
DIPLOPODA			1						
COLLEMBOLA									
Morulina nr. *gigantea*					8	1	20	1	2
Entomobrya nivalis	3	2	77	3	9	135	55	50	202
Isotoma spp.	32	33	25	51	80	230	155	112	378
Tomocerus flavescens	20	45	41	39	3	1	5	5	0
NEUROPTERA	2	2	1	1				2	
HOMOPTERA									
Psylla americana						1			1
Aphididae						2		2	
Pseudococcidae	1	7	1	10		1	1		
COLEOPTERA									
Carabus taedatus						1		1	
Staphylinidae						1		2	
Cantharidae (lar)		4	1	2		1		5	1
Byrrhus sp.							1		
others	1	3		3		2		4	1
LEPIDOPTERA									
Rhopalocera (ad)					1		1		
(lar)	1		1						
Noctuidae (ad)		1							
(lar)	2	5	1	2	11	11	3	3	9
Nepticula spp.			5		3	14	23		18
others			1					1	
DIPTERA									
Bradysia spp.	83	112	77	68	48	162	289	261	972
Megaselia spp.	8	5	7	10	5	12	34	9	27
Anthomyiidae	7	12	10	4	3	11	8	20	38
others	1	6	20	1	8	14	8	5	4
HYMENOPTERA									
Tenthredinidae (ad)	1	1			1		1		
(lar)			1			1	1		
Braconidae	1	1	1	4	1	1	2		2
Ichneumonidae	14	7	12	15	12	14	14	6	15
Chalcidoidea		2	7	1	2	5	5	3	4
Proctotrupoidea	4		3	1		2	1		1
Bombus spp.	8	2	5	2	1	7	2	5	3
ACARINA									
Parasitoidea	3	7			4	14	1		
Podothrombium malignum	59	162	42	73	28	22	80		221
Microtrombidium sp.		5	2	1	1				
ARANEA	85	112	130	39	45	72	59	87	100

NOTE: Trap no. 117 on bare shale, traps no. 115,116,118 in *D. octopetala* mats.

[1]Stand no.6, p.71.
[2]Stand no.7, p.71.

were inadequately represented or were caught in approximately equal numbers on shale and conglomerate.

The conglomerate-based community was richer in plant species, and had a vascular plant cover twice as great as on shale (Table 15, p.71). It also had a much higher percentage of large rocks and of litter. The coarser surface provides greater surface stability and a fuller three-dimensionalization of the habitat; and the greater plant variety and cover, and resultant increase in litter, provide more escape and living space and more food for small arthropods.

Elevational relationships

In general, the numbers and kinds of organisms decrease with increasing elevation. In Tables 47 and 48, note the low values for most arthropod groups at the highest elevations. The only ones with comparable or higher numbers in traps here were *Isotoma* spp., *Podothrombium malignum*, and noctuid larvae. *Morulina* nr. *gigantea* and *Erythraeus* sp., two arthropods abundantly trapped in the lower alpine zone, were totally absent from high-altitude catches. Certain insects, trapped in very low numbers at the highest elevation but absent elsewhere, probably flew up or were blown up.

Spiders in the Bald Hills form a good group in which to investigate altitudinal relationships in arthropods:

1) They can be caught in reasonably large numbers, for they are fairly abundant as well as mobile.
2) They entail a relatively large number of species.

TABLE 47. Mean numbers of arthropods of certain groups collected in pitfall traps in different plant communities, 1971. Values adjusted to represent the average microhabitat in each community.

COMMUNITY	*Artemisia norvegica*/ *Salix arctica* (2225m)	*D. octopetala*/ lichen (2250m)	*D. octopetala*/ *Cassiope tetragona* (2530m)	*D. octopetala*/ lichen (2590m)
COLL. PERIOD	11 July-10 Oct	28 May-10 Oct	6 June-10 Oct	6 June-10 Oct
Morulina nr. *gigantea*	15	8		
Entomobrya nivalis	4	25	9	15
Isotoma spp.	7	36	56	73
Tomocerus flavescens	31	8	94	3
HOMOPTERA	56	1	1	+
Carabidae	14	2	1	
Staphylinidae	30	2	1	
other COLEOPTERA	4	4	+	2
Noctuidae (lar.)	1	1	2	10
Nepticula spp.		22	2	+
ICHNEUMONOIDEA	22	13	12	8
CHALCIDOIDEA	7	4	2	1
PROCTOTRUPOIDEA	16	1		
Bombus spp.	19	8	3	3
Erythraeus sp.	2	145		
Podothrombium malignum	159	137	15	197
Microtrombidium sp.	4	10	7	50?
PARASITOIDEA		7	6	+
ARANEA	66	36	45	9

+<0.5

TABLE 48. Mean numbers of arthropods of certain groups collected in pitfall traps in different plant communities, 11 June - 10 Sept 1972. Values adjusted to represent the average microhabitat in each community.

COMMUNITY	*Phyllodoce-Cassiope mertensiana* (2225m)	*Dryas*/ lichen (2250m)	*Dryas*/lichen (2350m)		cushion-rosette[1] (2320m)	*Cassiope tetragona*/ *Dryas*[2] (2530m)	*Dryas*/ lichen[2] (2590m)
			shale	conglomerate			
Morulina nr. *gigantea*	42	11		4			
Entomobrya nivalis	5	76	66	113	190		
Isotoma spp.	16	60	27	240	29	28	62
Tomocerus flavescens	37	21	40	3		57	3
NEUROPTERA			1	1			1
Grylloblatta campodeiformis		+	+			+	
Pseudococcidae	2	1	2	1		2	+
other HOMOPTERA	25	+		2	+		+
Carabidae	5	3		1	1		
Staphylinidae	1	1		1	2	2	+
other COLEOPTERA	1	5	2	4	1	1	+
Noctuidae (lar.)	1	5	1	7	14	4	6
ICHNEUMONOIDEA	3	28	12	14	10	+	3
CHALCIDOIDEA	3	18	7	5	2	+	+
PROCTOTRUPOIDEA	3	1	3	2	4		+
Bombus spp.	7	3	5	4	4	+	2
Anthomyiidae	10	23	10	20	3	1	3
Erythraeus sp.	27	55					
Podothrombium malignum	16	146	38	86	13	18	62
Microtrombidium sp.	6	21	12			-	-
PARASITOIDEA	7	2	1	4	4	8	4
ARANEA	100	43	123	80	25	-	12

[1] bare shale not sampled
[2] 11 June - 11 August
+<0.5

3) They are apterous and thus less likely to occur outside their normal habitats.

There was a negative correlation between altitude and number of spider species (Fig. 29). The highest elevations

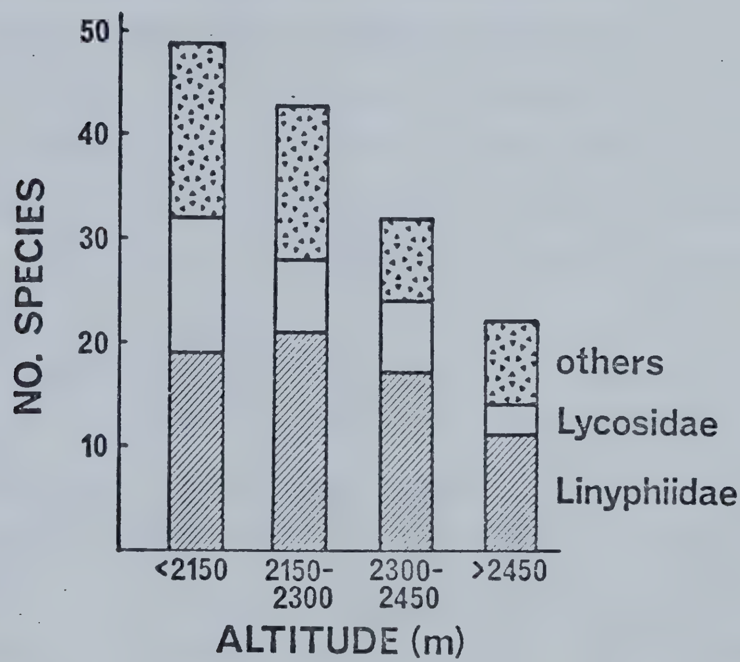

FIG. 29. Numbers of spider species in relation to altitude in the Bald Hills.

had less than half the species near timberline. It should be noted that no forb meadows were represented in the higher-elevation collections. Local meadow pockets here might harbor a few additional species.

The largest group was in the forest-tundra zone and comprised two basic elements: (1) eighteen cases of singletons or very few specimens, implying subalpine species at their

upper altitudinal limit; and (2) ten forest-tundra species, abundant in this zone but not straying much above it. Also present were a few alpine strays, and eleven wide-amplitude alpine species. In the forest-tundra zone these were trapped only in the tundra sections of the landscape.

The second group, in the low alpine zone, was only slightly smaller than the first. It included a few strays from the forest-tundra zone, and a large number of *bona fide* tundra species such as *Xysticus labradorensis*, *Dictyna borealis*, *Cochlembolus alpinus*, *Cornicularia karpinskii* and *Typhochraestus pygmaeus*.

Progressive reductions in species number were recorded in the third and fourth groups. Five of the Bald Hills species were found in only these groups but this is not significant because some of them, e.g. *Melocosa* and *Aculepeira*, could occur in suitable habitats at lower elevations. The only species that might typify a high or xeric-alpine fauna are *Cornicularia karpinskii*, *Erigone zographica*, *Islandiana alata*, and *Oreonetides vaginatus*.

Schmoller (1971a), working in a 500 m range above timberline in Colorado, reported a drop in the numbers of species of spiders and carabids at higher elevations. He could see no effect of altitude *per se* on the numbers collected in pitfall traps, whereas I noted dramatically smaller catch numbers of some arthropods including spiders at the highest elevations in the Bald Hills (Tables 47,48).

D. octopetala/lichen communities are floristically and

structurally similar at all elevations in the Bald Hills. Furthermore, the reaction of most arthropods to *D. octopetala* mats seems constant - the proportion trapped within mats vs. outside of mats seems comparable at different elevations (Table 39). Yet net arthropod activity is much lower at the highest elevations. Stronger winds and lower surface temperatures may be the main factors responsible.

Microsite relationships

Plant cover and arthropod numbers

There is a positive correlation between very low percent plant cover and low numbers of arthropods of most groups (Tables 34,43). Collembola seem the only exception, mainly on the strength of *Folsomia quadrioculata* which had highest population levels on bare ground. Plant cover greater than 15-20% harbors much higher numbers of arthropods, mites in particular, than does very low cover (Table 43). But among higher-cover samples there is no apparent correlation between population numbers of any arthropod groups and percent cover of: *Dryas octopetala* (live); *D. octopetala* mats; vascular plant species; bryophytes; lichens; rocks and pebbles; litter; or any combination of the above.

The leveling off of mite numbers beyond ca. 20% plant cover is noteworthy. Given a greater surface area and volume of litter, i.e. a greater carrying capacity, one would anticipate a proportionate increase in mite numbers. Losses during extraction and a variable thickness of organic matter

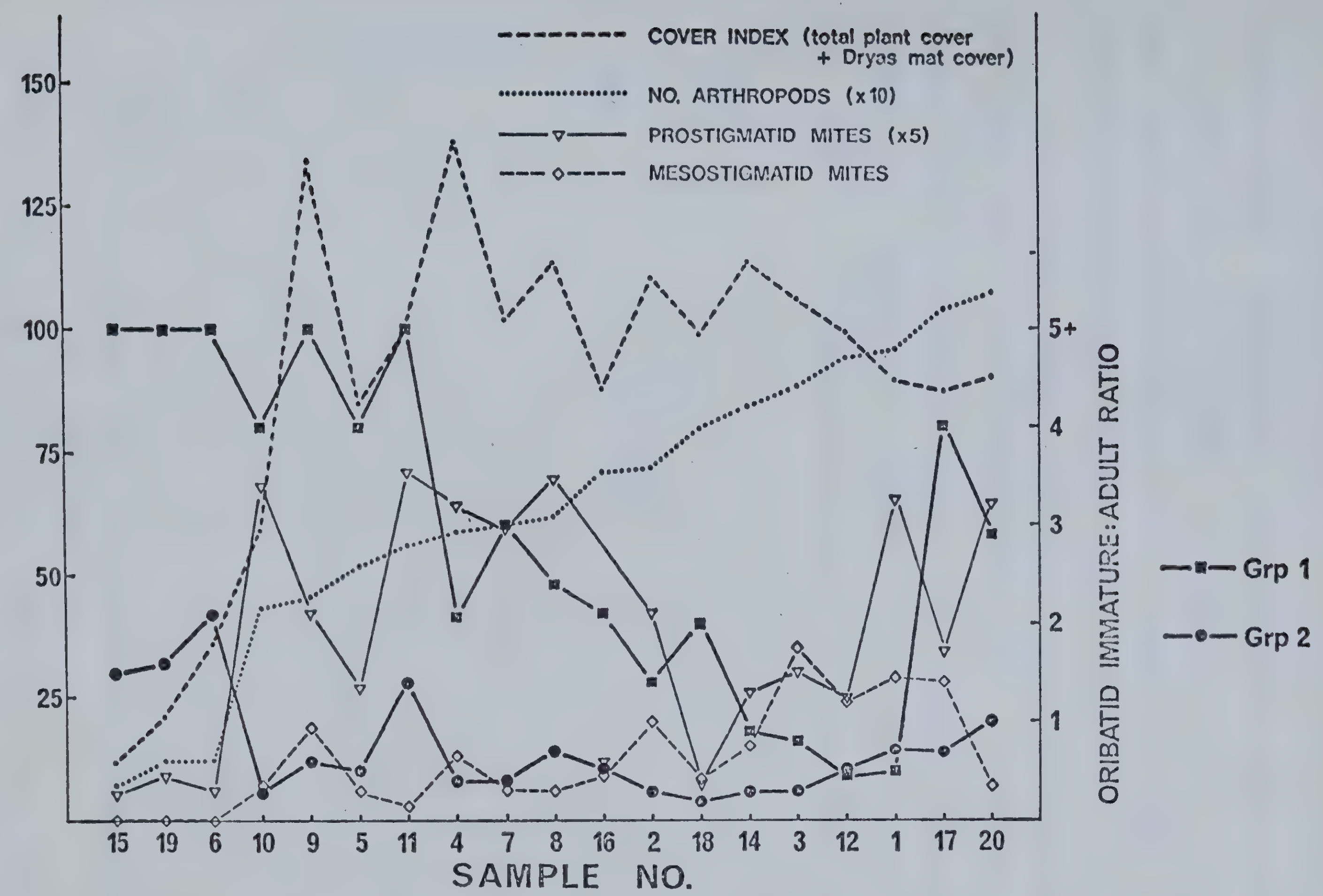

FIG. 30. Relationship between plant cover and numbers of certain arthropods in a *Dryas octopetala*/lichen community (stand 3). Samples (625 cm^2 each) collected on 20 Sept 1970, and arranged in ascending order of total arthropod catch.

between samples might account for some of the results. But they do not adequately explain the relatively equal numbers between samples. Certainly, mite numbers are not well attuned to percent cover of any plant or total plant cover. There even seems to be a decrease in mite numbers with very high cover of vegetation and organic matter (Fig. 30).

Collembolan populations showed very poor correlation with plant cover or mite numbers (Fig. 31). Evidently Collembola occur in "pockets" rather than randomly. Dense or areally large aggregations seem to be the exception. A sampling size of 1 m^2 might produce much more comparable numbers,

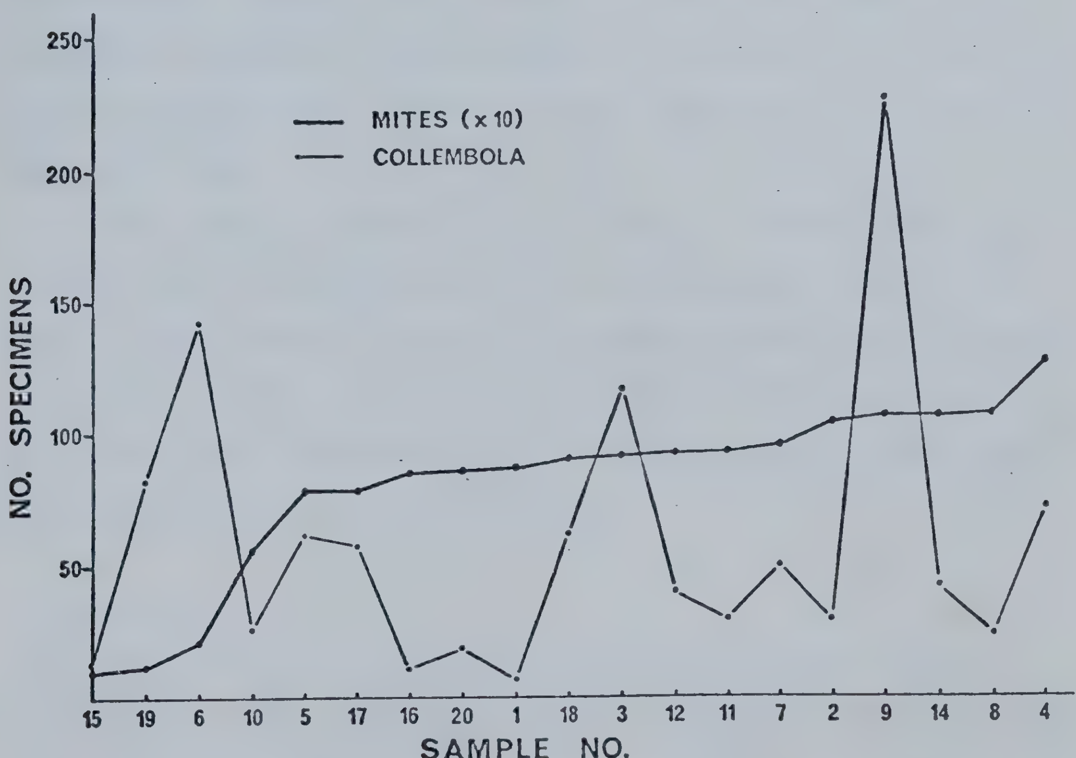

FIG. 31. Numbers of mites and collembolans extracted from 625 cm^2 surface samples in a *Dryas octopetala* /lichen community (stand 3), 20 Sept 1970.

by dampening the small-scale pattern of contagious distribution. Edwards and Fletcher (1971) suggest a sampling unit of 10-25 cm^2 for Collembola, but this seems much too small.

Sample no.9 (Table 43) exemplifies the contagion of tundra populations. This sample had many mirid nymphs, numbers of fly larvae, a large pocket of *Proisotoma*, and a pocket of the oribatid *Hungarobelba*. The plant cover was quite undistinguished qualitatively or quantitatively.

The immature:adult ratio of oribatids was higher under conditions of sparse plant cover. This suggests a flow of young mites from *Dryas* mats onto gravel patches, possibly a consequence of saturation pressure. Their sustenance in the peripheral habitats is not assured and they must be viewed as surplus, unimportant compared to the large nuclear populations within the mats.

The immature:adult ratio of grp.1* oribatids averaged 3:1 through most samples (Fig. 30), and the grp.2 ratio was 0.5:1. There seemed to be a correlation between grp. 1 and 2 oribatids in their immature:adult ratios. No strong correlation was apparent between numbers of Mesostigmata, Prostigmata, grp.1 oribatids, or grp.2 oribatids.

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*Grandjean (1954) prepared a provisional classification of the Oribatei. Three of his eleven assemblages are represented in the Bald Hills. Brachychthoniidae belongs to one; Nothridae, Camisiidae, Trhypochthoniidae and Malaconothridae to a second; and all others (Appendix 2) belong to a third. I have combined the first two and call them grp.1; his last assemblage I call grp.2. The grp.1 mites, generally larger and more rectangular in form than grp.2 mites, are easily separated under 20-30 magnification. The two may conform to Oribatei Inferiores and Oribatei Superiores respectively (Woolley 1971).

Pitfall trapping in different microsites

Microsite relationships were also investigated through pitfall trapping. The major difficulty in interpreting results is that arthropods may behave quite differently in unlike microhabitats. Spiders, for example, are probably more active on a bare surface than in a vegetated patch, because 1) they are less constricted in their movements and 2) they probably seek shelter and will move faster outside it. Thus the numbers of spiders and other arthropods trapped on bare patches may be overestimated in relation to vegetated sites.

The most important microsite studies were conducted in a terracette *Dryas octopetala*/lichen community (stand 3, Table 15). The three basic microhabitats investigated were gravel patches (terracette tops), *D. octopetala* mats, and mossy hollows. *Empetrum nigrum* mats were also included in 1971 and 1972.

Some arthropods, e.g. most beetles, were not trapped in sufficient numbers to show a microsite bias (Fig. 32). Hymenopterans were trapped in much lower numbers in the hollows (Table 39, Appendix 11). Most flies were caught in about equal numbers in all microhabitats (Table 39). In all three years of study, *Bradysia* was caught in larger numbers in *D. octopetala* cover than on bare gravel (Table 39, Appendix 11). Does this indicate that *Bradysia* prefers to swarm over *Dryas* cover, or that it seeks shelter in *Dryas* mats when it gets windy?

Arthropods ideal for microhabitat study were active apterous species trapped in relatively high numbers. Two

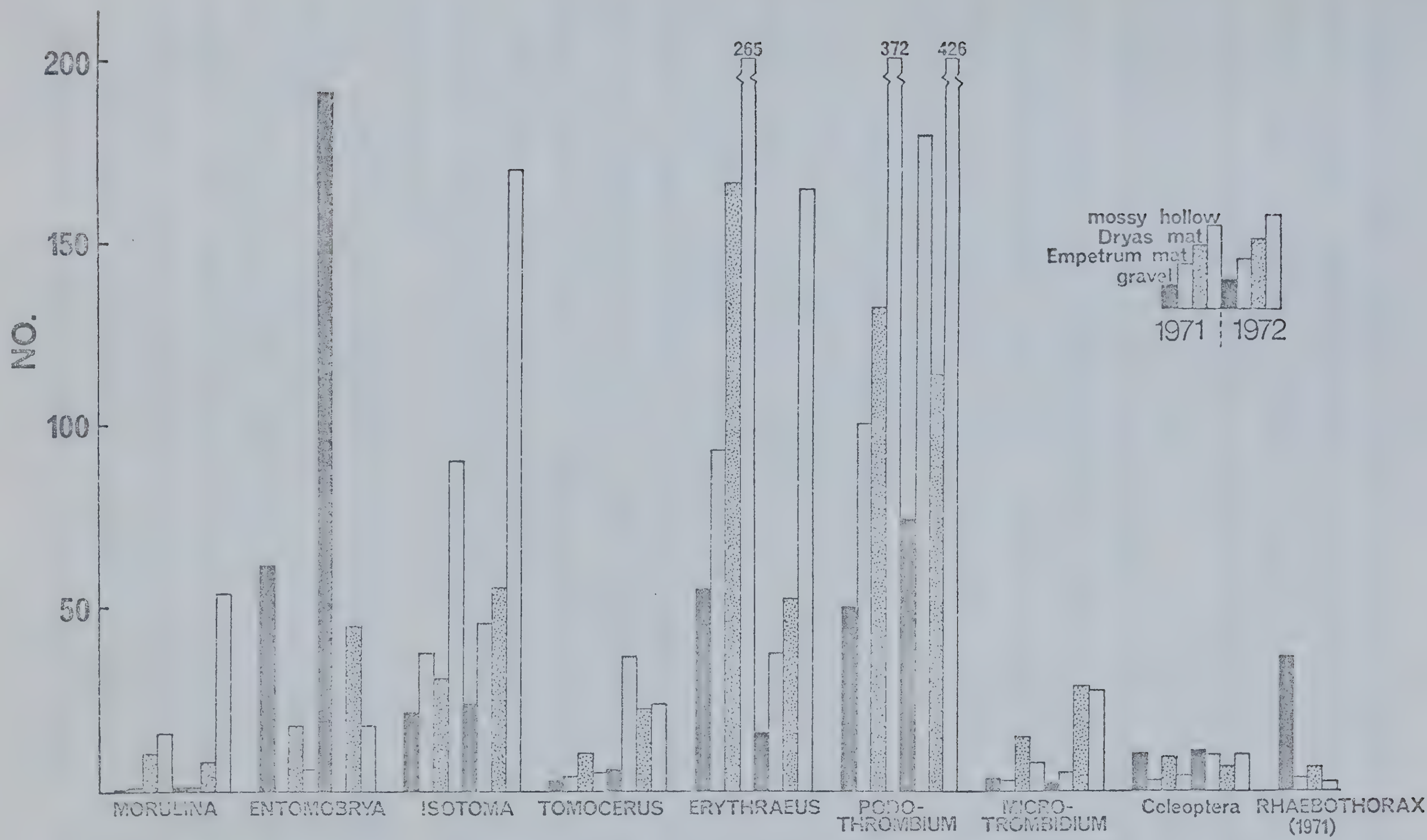

FIG. 32. Mean numbers of certain arthropods collected in pitfall traps in four microhabitats of a *Dryas octopetala*/lichen community (stand 3), 1971 & 1972.

species of mites, several collembolans and some spiders fit this category. Most exhibited clear and usually consistent differences in numbers trapped at each microsite. *Entomobrya nivalis* and *Rhaebothorax* n.sp. seemed virtually restricted to gravel patches (Fig. 32, Table 39). All others were trapped in highest numbers in the mossy hollows (even though mobility is presumably most restricted here) and least abundantly on the gravel patches (Fig. 32). The pattern was consistent between years except for some of the 1970 catches, but these missed early-season activity.

Empetrum nigrum mats had very low catches of most arthropods (Fig. 32). Even *Entomobrya nivalis* avoided *Empetrum* about as much as it did mossy hollows. We thus have the peculiar situation of many arthropods shunning *Empetrum* mats despite the thick, presumably sheltering layer of stems and leaves. Extraction samples in the forest-tundra zone yielded lower numbers of mites from *Empetrum* than from *Dryas* mats (Table 34). Pitfall traps in two mats near an *Abies* clump had contents comparable to those of nearby traps in other types of cover (Table 45).

The overall impression is that *Empetrum* is faunistically depauperate compared to *Dryas*. Litter within *Empetrum* mats seems poorly decomposed, comprising hard and blackened, intact leaves. This could be the key to the poor development of its microfauna and the reluctance of many organisms to even enter it. One animal that definitely preferred *Empetrum* mats in the study area was the spider *Arctobius agelenoides*. Its webs

were abundant in mats in the forest-tundra zone. *Arctobius agelenoides* is a fairly large spider compared to most tundra species, and it might require the sizeable space that *Empetrum* provides between the leaf mass and the ground surface.

Seasonal trends

Most arthropod groups in the Bald Hills exhibit definite peak periods of activity. Some organisms, e.g. *Nepticula* and a species of mite (Parasitoidea), peak in the earliest part of the season (Tables 37,38). Many arthropods peak in July: beetles, noctuid larvae, most flies, and the mites *Erythraeus* sp. and *Podothrombium malignum*. Peaking later in the season are parasitic hymenopterans. As in arctic tundra (MacLean and Pitelka 1971) their emergence is delayed to allow time for sufficient host development. Peak arthropod activity is not synchronous with peak *Dryas* activity. The seasonal development of arthropods of most groups probably begins in late May - early June. But *D. octopetala* has completed much of its growth, and has finished flowering, by the time most arthropods begin moving around much.

There is no strong seasonal peak in spider activity (Tables 37,38), but the majority of species seem most active in late July - early August. Males and females of some species exhibit unlike patterns of activity. In some, e.g. *Pardosa* spp., the males show an early-season burst of activity whereas the females are more active toward fall. This is in general agreement with observations by Leech (1966) who found

non-synchronous peak activity in males and females of some high-arctic species.

Two large cursorial mites, *Erythraeus* sp. and *Podothrombium malignum*, were very active in many of the same habitats at lower elevations. If both compete for the same resource, one would expect two peaks of seasonal activity. Both peak at about the same time (Fig. 33), suggesting incomplete competition at best. The temporally varying response to microhabitat by these mites is notable. As the season progresses, there is a tremendous increase in catches of both *Erythraeus* and *Podothrombium* in mossy hollows, then a violent decrease in late Aug. - early Sept. Those in *Dryas* mats and gravel patches exhibit much more moderate rises and falls. These data suggest that *Dryas* mats and gravel patches have a limited carrying capacity for mites at all times of the season, whereas mossy hollows have a high carrying capacity in mid-summer compared to early or late summer. Two conclusions are possible: 1) Mites migrate to the mossy hollows in mid-summer leaving stable populations in other parts of the tundra. 2) Mites develop at a much faster or higher success rate in the mossy hollows. They show some dispersal (e.g. mid-summer peaks of mites in *Dryas* mats and gravel patches in 1971), but most individuals remain in the hollows.

Collembolans of the genus *Isotoma* exhibit a similar seasonal pattern (Fig. 33). *Entomobrya nivalis* is trapped almost exclusively on bare gravel in the off-season (Fig. 33). In July and August numbers are also trapped in *Dryas* mats and

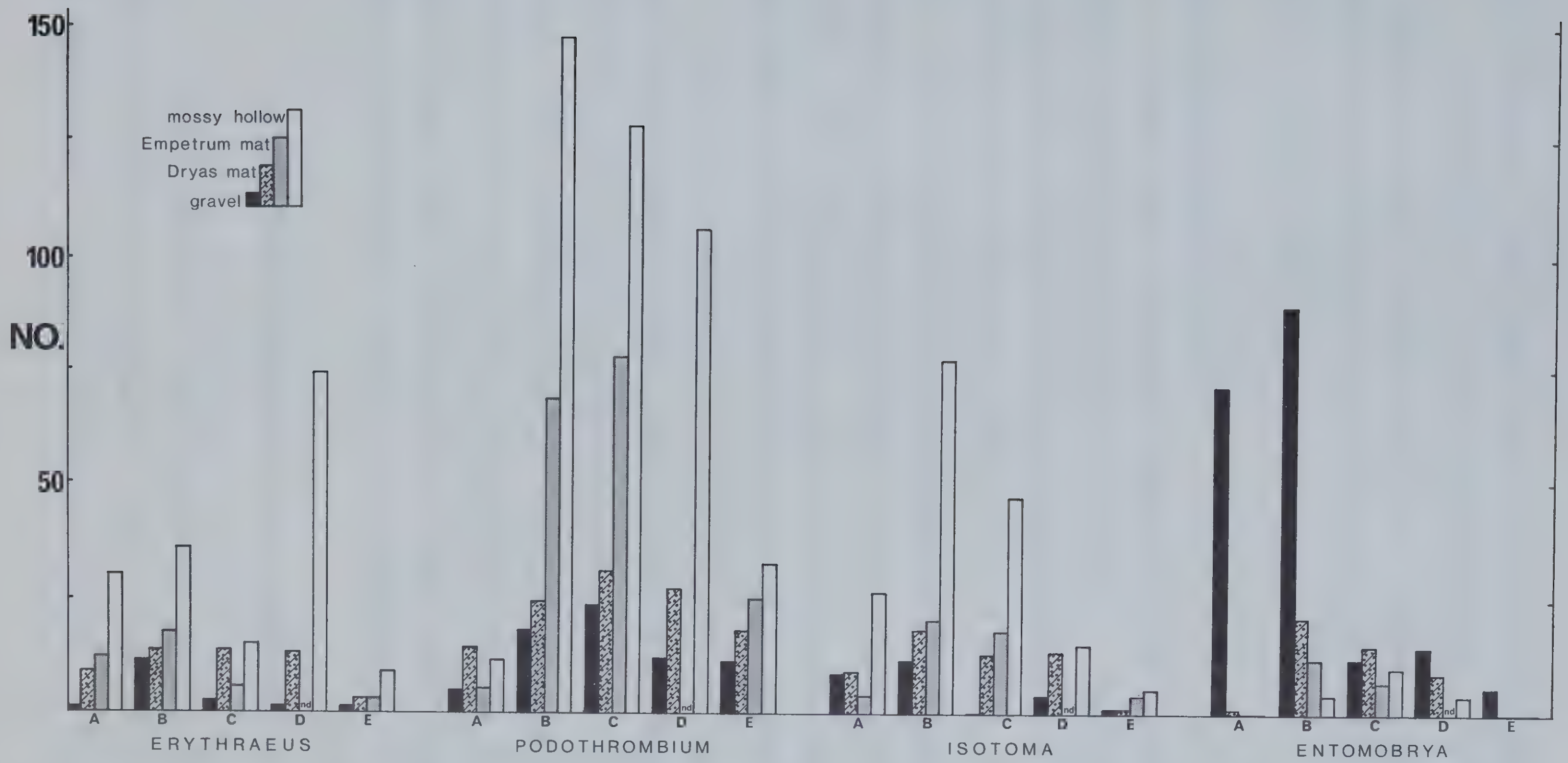

FIG. 33. Seasonal trends in mean numbers of the mites *Erythraeus* sp. and *Podothrombium malignum*, and the collembolans *Isotoma* spp. and *Entomobrya nivalis*, collected in pitfall traps in different microhabitats of a *Dryas octopetala*/lichen community (stand 3), 1972. A=11 June-11 July, B=11-27 July, C=27 July-11 Aug, D=11-27 Aug, E=27 Aug-10 Sept.

mossy hollows. The significance of this is unclear.

The seasonal trend of relative numbers of Collembola, or relative numbers of the two mites, shows no pattern. The numbers of trapped mites and collembolans of different species do not rise and fall proportionately.

Year-to-year variability

There was a dismaying variability in arthropod catches between the three years of investigation. The early-season activity was missed in 1970, but the numbers are still very low (Table 45) compared to 1971 and 1972 (Table 39, Appendix 11). Just one season's investigations may lead one to wholly erroneous conclusions regarding arthropod activity in alpine tundra. Even three years' work is not enough, though it does give some idea of the range of variability between years.

It is not possible to draw up correlations between year-to-year animal numbers and any factors. Weather would be implicated, and predator-parasite cycles would also be involved. For phytophages and detritus feeders, the food supply itself is no problem, for it seems more than adequate during the growing season. The problem is more one of being able to function efficiently enough to use this food.

OTHER TUNDRA VEGETATION AND ARTHROPODS

Dryas octopetala tundra compares favorably in arthropod diversity with other vegetation types in the Bald Hills. It has comparable or higher levels of activity in most groups

including flies, Hymenoptera, Collembola, spiders and mites (Tables 39,45, Appendix 11). Spider species richness seems maximal in the *D. octopetala*/lichen community. Herb meadows, by contrast, have few species but many individuals, mostly *Ceraticelus* and several *Pardosa* species. At Barrow, Alaska, Bohnsack (1968) found spider numbers highest in moist meadows.

Cushion-rosette tundra has much lower numbers of arthropod species and individuals than *Dryas* tundra. Major activity is provided by: (1) flies and Lepidoptera, usually scouting for flowers; (2) noctuid larvae, inexplicably active on bare shale pebble surface; (3) *Entomobrya nivalis* (Table 39). On a per unit area basis, cushion and rosette plants may have mite numbers comparable to those of *D. octopetala* mats (Tables 35,41); but the very low percent plant cover in cushion-rosette communities disallows the establishment of large arthropod populations.

Dryas tundra has lower beetle activity and very few bugs compared to more mesic communities (Tables 45,47,48). The relatively mild environments and higher productivity of herb meadows are rather unlike those of most tundra communities, so it is no surprise to find good representation by insect groups (e.g. beetles) more typical of temperate than arctic latitudes. At a tundra site in Alaska, Hurd and Lindquist (1958) found the greatest variety and numbers of terrestrial arthropods in more heavily vegetated substrata, especially where the vegetation was diverse; and the lowest where the habitat was ecologically simple or similar throughout. Vertical stratification of arthropods may contribute

to the large numbers and variety in meadow compared to typical tundra (Chernov 1971). However, numbers of oribatids may be much lower in herb meadows than in *Dryas*-dominated tundra (Chernov 1971). Relatively low numbers of mites were collected in herb meadows in the Bald Hills (Table 35).

The simplest plant communities, e.g. *Lepraria* surface and *Eriophorum* meadows (Tables 34,35), had fewest kinds of organisms, mostly oribatid mites, but highest numbers. *Arctostaphylos uva-ursi* had high arthropod numbers but the most dissimilar fauna compared to normal tundra communities. *Kobresia bellardii* had high numbers of: prostigmatid mites especially Tydeidae, Bdellidae, Erythraeidae, Trombidiidae; collembolans especially *Isotoma* spp.; and spiders. The combination of exposed site but thick turf may be significant. Although relatively simple in structure, *Kobresia* meadow is near the top end of arthropod diversity and density among tundra community types.

D. octopetala mats isolated in other vegetation retain their faunistic integrity fairly well. In Table 35, note only half as many mites in a *Dryas* mat as in surrounding *Kobresia* turf; and the higher numbers of mites but lower numbers of insects in the *Dryas* mat surrounded by forb meadow. In these and other ways the *Dryas* islands resemble normal *Dryas* tundra. This conforms with observations in W Taimyr by Chernov (1971), that microsites or community fragments will have an invertebrate composition similar to that of the community they resemble, rather than the one in which they lie.

9. DISCUSSION AND INTEGRATION

PHYTOGEOGRAPHIC RELATIONSHIPS OF BALD HILLS BIOTA

Arctic and alpine affinities

The Bald Hills area has fairly close biotal affinities with tundra in both arctic and alpine areas of western North America. Graminoid-dominated communities prevail in the U.S. Rockies (Cox 1933, Hayward 1952) whereas dwarf shrubs are most important in the Canadian Rockies (Beder 1967, Hrapko 1970, Trottier 1972). The extensive hydrophytic graminoid communities of arctic lowlands and coastal plains (Bliss et al. 1973) find their counterpart in only small pockets in alpine tundra. But upland arctic communities, particularly those dominated by dwarf heaths and lichens, have very well developed analogues in the Canadian Rockies. Such communities are depauperate and relatively insignificant in the U.S. Rockies. Xeric cushion-rosette and lichen tundra communities in the Canadian Rockies have their counterpart in High Arctic areas of Polar Semi-Desert (Bliss et al. 1973). Thus, although floristically the Bald Hills are more like the rest of the Rocky Mountains (Tables 49,50), in community structure and dominants they resemble upland arctic tundra.

In terms of floristic richness, viz. numbers of vascular plant genera and species, the Bald Hills and other tundra sites in the Canadian Rockies compare favorably with other alpine as well as arctic areas in North America.

TABLE 49. Floristic similarity[a] of the Bald Hills to some other tundra areas in North America.

LOCALITY	SOURCE	VASCULAR PLANTS		MOSSES		LICHENS	
		gen.	sp.	gen.	sp.	gen.	sp.
Colorado alpine zone	Marr 1967, Weber & Willard 1967, Weber 1973	63	37	85	52		
Barrow, Alaska	Murray & Murray 1973	54	20	70[b]	35[b]	75	39
Truelove Lowland, Devon Island, N.W.T.	Barrett & Teeri 1973, Vitt 1975, Barrett 1972	47	22	63	33	71	45
Lake Hazen, Ellesmere Island, N.W.T.	Savile 1964, Brassard 1971	53	25	69[c]	43[c]		
Canadian Arctic Archipelago	Porsild 1964, Brassard 1971	64	27	71	41		

[a]Percent similarity = $\frac{2w}{a+b}$, where w = no. taxa in common, a & b = no. taxa in each of two areas.

[b]Includes hepatics.

[c]All of Ellesmere Island.

TABLE 50. Percent of Bald Hills plant taxa found in tundra of Colorado and the Canadian Arctic Archipelago.

PLANT GROUP		COLORADO ALPINE[1]	CANADIAN ARCTIC ARCHIPELAGO[2]
vascular plants	gen.	78.7	77.5
	spp.	51.1	43.9
mosses	gen.	100.0	100.0
	spp.	68.4	69.5
lichens	gen.	100.0	92.7
	spp.	76.0	82.6

[1]Based on Marr 1967, Weber and Willard 1967, Weber 1973, Shushan and Anderson 1969.

[2]Based on Porsild 1964, Brassard 1971, Lynge 1947, Hale 1954, Barrett 1972.

They are not as rich in lichens as arctic areas (e.g. Hale 1954, Barrett 1972), but richer than the central and southern Rockies (e.g. Bamberg and Major 1968, Shushan and Anderson 1969). Bryophyte richness seems comparable throughout the geographical range, though tundra bryophyte cover is lower in the central and southern Rockies (cf. Bliss 1956, Weber 1973).

About 70% of the Bald Hills vascular plant species fall into 9 families, some of these among the most important in alpine areas through Europe and North America. Although adaptation to the alpine environment has been accomplished by a fairly large number of angiosperm families, Packer (1974) suggests that alpine tundra through much of the world has only a few families of overall significance, viz. Compositae, Cyperaceae, Gramineae, Rosaceae, Scrophulariaceae, Ericaceae, Caryophyllaceae, Ranunculaceae, Leguminosae, Cruciferae.

The vertebrate fauna of the Bald Hills has strong affinities with that of the rest of the Rocky Mountains, closer certainly than with Arctic. The invertebrates, on the other hand, evidently correlate quite closely with those of arctic tundra. Many of the same insect genera and species occur throughout (cf. Hurd and Lindquist 1958, Oliver et al. 1964, Kevan 1970, Ryan 1972). Brinck (1974) states that the invertebrate families inhabiting alpine habitats are very much the same all over the world.

Compared to arctic tundra, the Bald Hills have a

relatively rich arthropod fauna (Table 51). In both there is a preponderance of flies (Downes 1964, MacLean and Pitelka 1971). Also amply represented are mites, collembolans and parasitic hymenopterans. The Bald Hills are much richer in spiders (Table 51). The Arctic is richer in chironomids which comprise up to 35% of the arthropod fauna (Hurd and Lindquist 1958, McAlpine 1964, Oliver et al. 1964, Danks and Byers 1972). The ratio of insect to vascular plant species is very low (ca. 1:1) in the High Arctic (cf. McAlpine 1964, Ryan 1972), but ca. 3:1 in Low Arctic. It is ca. 3:1 in the Bald Hills. In temperate areas it is more like 10:1 (Lindroth 1965).

The arthropod component of Colorado alpine tundra is generally comparable, in the main groups anyway, with that of the Bald Hills (cf. Schmoller 1971c), but not enough is

TABLE 51. Estimated arthropod fauna of the Bald Hills and several arctic sites.

LOCALITY	SOURCE	NO. ARTHROPODS	NO. SPIDERS
Bald Hills		600	70
Barrow, Alaska	Bohnsack 1968	450	38
Lake Hazen, Ellesmere Is., N.W.T.	Downes 1964, Leech 1966	300*	13
Devon Is., N.W.T.	Ryan 1972	200	8
Bathurst Is., N.W.T.	Danks & Byers 1972	150	4
Ellef Ringnes Is., N.W.T.	McAlpine 1964	50	2

*Insects only.

yet known for detailed comparisons. The most significant disparity is the abundance in the U.S. Rockies of ants and grasshoppers (Alexander 1951, Hayward 1952, Gregg 1963, Schmoller 1971c), two groups virtually absent from the Bald Hills. Some alpine insect faunas have 50% or more apterous and vestigial-winged species (Mani 1968), but only ca. 5% of the Bald Hills insects are flightless. They are *Chionea*, *Oreadomyia*, *Grylloblatta*, some parasitic hymenopterans (*Stemmatosteres*, *Monoctonus*, *Ceraphron*, *Cirrospilus*, *Trimorus*, *Agrothereutes*, *Gelis*), and possibly some beetles.

Relative impoverishment of Canadian Rockies alpine biota

In a broad biogeographical perspective, alpine and arctic tundras have depauperate invertebrate faunas (Downes 1964, Lindroth 1965, Mani 1968). The Bald Hills tundra has been invaded by only one or a handful of species in some groups that are well represented in temperate and tropical ecosystems, viz. phalangids, millipedes, centipedes, ants, thrips, mirids and grasshoppers. Beetles are also relatively poor in species and numbers, especially in upland tundra; this despite Mani's (1968) insistence that beetles are the most important high-altitude insects in all parts of the world. Tundra floras are also relatively depauperate (Billings and Mooney 1968, Packer 1974), though some more so than others. Although comparable in richness to many North American alpine floras, the Canadian Rockies flora is much poorer than many alpine floras in mid-temperate latitudes (cf. Major and Bamberg 1967).

Not only does Canadian Rockies tundra have relatively few species, it has a very low content of endemics (Packer 1971). This is normal for higher-latitude mountain biotas (Brinck 1974), and contrasts with some mountain regions, e.g. the Himalaya (Mani 1962) and Colorado Rockies (Alexander 1951, Schmoller 1971c) with distinctive species and indeed genera of alpine invertebrates; and numerous mountain areas, e.g. Sierra Nevada of California (Major and Bamberg 1967) and the Swiss alps (Schroeter 1926) with sizeable autochthonous floras.

One reason for the low endemism in the Canadian Rockies may be the lack of major barriers to the Arctic. Brinck (1974) notes that the insularity of northern mountains is very low, whereas in the Pyrenees, Alps and many other mountains at intermediate latitudes, ecological and geographical isolation are greater and the ecosystems are also older. The relatively impoverished Canadian Rockies alpine flora may be in part attributed to the extensive forests below the alpine zone (Packer 1974). There is no proximal source of preadapted species for the generally cold, dry, and light-rich alpine habitat. Alpine floras in Asia, derived from steppe or sparsely wooded highlands, are much richer (Tolmatchev cited in Packer 1974). The chief explanation for the relatively undistinguished Canadian Rockies biota is probably the recent glaciation that covered virtually all of the area. Southwest Alberta and adjacent areas of B.C. and Montana constituted one probable refugial area

(Packer 1971), and a handful of alpine endemics are a reflection of this. After deglaciation, reciprocal migrations occurred between Beringian and southern (U.S. alpine) refugia, but many U.S. alpine species and ecotypes have not yet migrated far across the old glacial boundary into Canadian mountains (Billings 1974).

ECOLOGY OF BALD HILLS VEGETATION

Environment

The Bald Hills tundra environment seems more maritime than continental. The most significant feature is the high frequency of freeze-thaw cycles, up to 40% in July and August in some sites, and generally 15-20% in most sites (Table 8). In the Olympic Mts. of Washington, Kuramoto and Bliss (1970) recorded almost 50% cycles in a timberline site with cold-air drainage. Continental alpine sites seem to have few freeze-thaw cycles in July and August. At Niwot Ridge, Colorado, freeze-thaw cycles are normally confined to spring and fall (Fahey 1973). On Plateau Mt. in Alberta, Bryant and Scheinberg (1970) reported a mean monthly frequency of 1 and 6 cycles in July and August respectively, but 15 and 11 in June and September respectively. On Signal Mt. in the Maligne Range, Hrapko (1970) recorded 3 cycles in July and 1 in August, in the exceptionally warm 1967 season.

By most other criteria the Bald Hills environment is relatively mild. Mean and maximum windspeeds through the year are low compared to other alpine sites (Judson 1965,

Bliss 1971), the winters are relatively mild compared to nearby subalpine sites and to alpine sites in other regions, winter precipitation is not high, summers are cool with generally low vapor pressure deficits, and congeliturbation processes are localized or small-scale.

Plant communities

"All over the world the main alpine habitats are the same, viz...exposed rock surfaces and stone and gravel fields characterized by strong solifluction,...sedges and grass heaths, shrub heaths, shrub thickets, bogs (mires), stagnant water bodies, and running water. The plant communities change with the area, but the physiognomic aspect is much the same" (Brinck 1974). The last four habitats are relatively unimportant in the Bald Hills. Most of the vegetation is dominated by dwarf shrubs (Appendix 4); there are also graminoid and forb meadows, and rocky, sparsely vegetated uplands. Four major vegetational Groups (Table 52) are recognized, based on growth-form and habitat, criteria used in many European and North American studies of tundra vegetation. The community types within each Group are characterized by dominant species in major strata. Important community types in the Bald Hills are *Dryas octopetala*/lichen, *Cassiope tetragona*/*D. octopetala*, *Phyllodoce glanduliflora*-*Cassiope mertensiana*, *Carex nigricans*, and *Artemisia norvegica*/*Salix arctica*.

Most Stony Tundra that lacked *Dryas octopetala* was characterized not on the basis of dominant species but by

TABLE 52. Major environmental relationships of plant community types in the Bald Hills.

MAJOR VEG. GROUP	PLANT COMMUNITY TYPE OR SUBTYPE	% COVER IN N HALF OF BALD HILLS[1]	ALTITUDINAL RANGE (m)	MAJOR ASPECTS[2]	WINTER SNOW ACCUMULATION (m)	SOIL TYPE[3]	HYDROLOGIC STATUS	FLOWERING PEAK
Stony Tundra	*Dryas octopetala*/lichen	9[5]	2125-2600	all,b,a	0-1	R,(B)	4-5	late June-early July
	D.o.-Arctostaphylos uva-ursi subtype	o	2300-2350	SE	0.5?			
	D. octopetala/Polytrichum piliferum	1	2075-2200	b	0.3-1	R,(B)	4	early to mid-July
	D. octopetala/moss	o	2325	N	2?	R	4	late July
	Artemisia norvegica/D. octopetala	1	2200-2300	S	0.5-1	R	4	early July
	Cushion-rosette	4	2100-2600	all,a	0-3	R	4-5	June-July
	Erysimum pallasii-Ranunculus gelidus subtype	P	2250-2400	SW,W	<0.5?			early to mid-June
	Vegetation stripe subtype	P	2300-2400	W	<0.5?			mid- to late June
	Cliff-ledge subtype		2100-2600	all				July
	Lichen tundra	7	2100-2600	a,all	0-1	R,rock	5	
	Kobresia bellardii	P	2250-2400	S,a	0.2?	R,B?	4-5	June
Heath Tundra	*Cassiope tetragona/Dryas octopetala*	5	2100-2500	E,N,(W),b	0.5-1.5	B,R	4	early to mid-July
	Phyllodoce glanduliflora-Cassiope mertensiana	37	2000-2400	N,E,(W),b	2-3+	B	3	July
	Luetkea pectinata	P?	2100-2350	N,E,(W),b	3+	B	3	late July
Herb Meadow	*Artemisia norvegica/Salix arctica*	5	2100-2300	N,E,(S),b	1(-2)	B	3	July
	A. norvegica-Luzula parviflora	o	2225	b	1	B(G?)	2	early to mid-July
	A. norvegica-Anemone occidentalis	P	2150-2300	NE,SE	1-2+	CR	3	July
	A. norvegica-A. occidentalis/Phyllodoce subt.	P?	2200-2300	b	2-3?	B?	3	July
	A. norvegica-Antennaria lanata	P	2200-2350	E,SE	2-3+?	R	3-4	mid- to late July
Snowbed	*Carex nigricans*	2	2100-2450	N,E,(all)	3+	R?	4	late July
	Luzula snowbed	P	2125-2450	N,E	2-3+	R	4-5	late July?
	Poa cusickii	o	2300-2330	E	2?	R	5	
Other types	*Eriophorum polystachion/Calliergon sarmentosum*	P	2075-2250	b	1?	G	1	
	Sphagnum bog	P	1950-2250	b	2?	G	1	
	Salix barrattiana	P	1800-2100	b	2-3?	CR?,G?	2-3	
	Artemisia michauxiana-Rubus idaeus	o	2250	W	<0.5?	R	5	
	Populus tremuloides scrub	o	2000	SE	0.5?	R	5	
	Abies-Picea krummholz	3	2100-2300	SE,a	0.5-1	R	4-5	

[1] o = one stand only, P = <0.5% cover.

[2] a = ridge crests & hilltops, b = level or very gently sloping ground.

[3] B = Brunisol, G = Gleysol, R = Orthic Regosol, CR = Cumulic Regosol.

[4] 1 = soil very poorly drained, 2 = imperfectly drained, 3 = mesic, 4 = well drained, 5 = excessively drained.

[5] Much higher cover (ca. 30%) in S half of the Bald Hills.

NOTE: Percent of N half of Bald Hills covered by all the above vegetation types adds up to 74%. The rest is barren cliffs, scree and snowbeds. Treed sections of the forest-tundra zone were excluded from the tabulation.

dominant growth-form, and the subtypes on a habitat basis. The reason is that the vegetation represented herein was a seeming hodge-podge of species assemblages in a great range of relative abundances. In the Stony Tundra complex it may well be futile to attempt to distinguish distinct community types on a floristic or dominant-species basis. In the N Cascades, Douglas (1973) found high *beta* (between-community) diversity in what he termed "blockfield tundra" stands, and remarked on the notable lack of success in satisfactorily classifying them. In the High Arctic, Savile (1960) noted "the absence of clearly defined associations in the poorer habitats. The plants that are able to survive in such habitats generally occur randomly in any combination...In such regions it is advisable to describe the flora in terms of major habitats rather than by associations."

Dryas octopetala/lichen community type

A few *Dryas*-dominated communities in the Bald Hills are co-dominated by bryophytes or forbs, but in most others lichens form the most important associated component. The *D. octopetala*/lichen community type is the nodal type not only of *Dryas*-dominated tundra but of all upland tundra in the Bald Hills and probably the Canadian Rockies in general. Stands occupy boulder-strewn or gravelly but fairly stable ridge crests and gentle slopes of all aspects. Characteristic vascular plant species over most of the North American range of the *D. octopetala*/lichen community include *Festuca brachyphylla*, *Antennaria alpina*, *Arenaria obtusiloba*, *A.*

rossii, A. rubella, Polygonum viviparum, Sedum lanceolatum, Selaginella densa, and *Silene acaulis* (Table 53). Also characteristic are certain lichen species in the genera *Alectoria, Cetraria, Cladonia, Cornicularia, Thamnolia, Lecidea, Lecanora, Rinodina, Rhizocarpon, Umbilicaria.*

Although the overall structure of the *D. octopetala*/lichen community is similar across its range, the species composition varies (Table 53). In the Canadian Rockies we get *Salix nivalis, Agropyron latiglume, Luzula spicata, Poa alpina, P. grayana, Oxytropis campestris, O. podocarpa, Potentilla nivea, P. uniflora, Saussurea densa, Saxifraga bronchialis, Solidago multiradiata.* Many species in Arctic stands are absent from the Canadian Rockies; the same is true of many species in the central and southern Rockies. Some species extend partway down the Cordillera, e.g. *Vaccinium vitis-idaea, Campanula lasiocarpa, Pdicularis arctica, P. lanata.* A few occur only in the southern part of the Canadian Rockies, e.g. *Smelowskia calycina, Hedysarum sulphurescens.* A more rigorous delimitation of the *Dryas octopetala*/lichen community types would yield a more uniform species assemblage than is seen in the Canadian Rockies stands (Table 53).

Vegetation-environment correlation

Table 52 summarizes relationships of major factors of the physical environment to the Bald Hills community types. In the alpine zone, snow is generally held to be the key factor in the pattern and phenosequence of plant communities

TABLE 53. Vascular plant species of *Dryas octopetala*/lichen communities in different parts of North America.

STAND NO.	1	2	3	4	5	6	7	8	9	10	11	12
LATITUDE (N)	64°25	52°51	52°42	51°40	51°35	51°20 -35'	50°35	49°13	49°01 -04'	48°48	48°49	40°15
ALTITUDE (m)		2250	2250-2590			2150-2250	2260-2500	2140	2260-2440	2320-2470		3400-3650
DWARF SHRUBS												
Abies lasiocarpa	.	.	.	x	.	.	.	.	.	.	.	.
Arctostaphylos nevadensis	.	.	.	.	.	.	.	.	.	.	x	
Arctostaphylos uva-ursi	.	.	x	x	.	.	.	.	x	.	x	.
Betula ?glandulosa	.	.	.	.	x	.	.	.	.	.	.	.
Cassiope tetragona	x	x	x	x	.	x	.	.	.	.	.	.
Diapensia lapponica	A	.	.	.	.	.	.	.	.	.	.	.
Dryas octopetala	A	A	A	A	A	A	A	A	A	A	A	A
Empetrum nigrum	x	.	x	A	.	.	.	.	.	.	.	.
Eriogonum androsaceum	.	.	.	.	.	.	.	.	x	.	.	.
Eriogonum flavum	.	.	.	.	.	.	.	.	.	x	.	.
Juniperus communis	.	.	x	A	.	.	.	.	.	.	x	.
Ledum decumbens	x	.	.	.	.	.	.	.	.	.	.	.
Loiseleuria procumbens	A	.	.	.	.	.	.	.	.	.	.	.
Penstemon davidsonii	.	.	.	.	.	.	.	.	.	.	x	.
Penstemon procerus	.	.	.	.	.	.	.	.	.	.	x	.
Phyllodoce glanduliflora	.	.	x	A	x	x	.	.	.	.	.	.
Picea engelmannii	.	.	x	A	x	x	.	.	.	.	.	.
Pinus albicaulis	.	.	.	x	.	.	.	.	.	.	x	.
Potentilla fruticosa	.	.	.	.	x	.	.	x	.	x	x	.
Pyrola secunda	.	.	.	x	.	.	.	.	.	.	.	.
Pyrola uniflora	.	.	.	x	.	.	.	.	.	.	.	.
Rhododendron camtschaticum	x	.	.	.	.	.	.	.	.	.	.	.
Rhododendron lapponicum	x	.	.	.	.	.	.	.	.	.	.	.
Salix arctica	.	A	x	x	x	x	A	.	.	.	.	.
Salix chamissonis	x	.	.	.	.	.	.	.	.	.	.	.
Salix glauca	.	.	.	x	.	.	.	.	.	.	.	.
Salix nivalis	.	A	A	x	A	x	A	A	A	.	.	.
Salix phlebophylla	x	.	.	.	.	.	.	.	.	.	.	.
Salix reticulata	x	.	.	.	.	.	.	.	.	A	.	.
Salix rotundifolia	x	.	.	.	.	.	.	.	.	.	.	.
Salix vestita	.	.	.	.	.	x	.	.	.	x	.	.
Shepherdia canadensis	.	.	.	x	.	.	.	.	.	.	.	.
Sibbaldia procumbens	.	.	.	.	.	x	x	x	.	.	x	.
Vaccinium scoparium	.	.	.	x	.	.	.	.	.	.	.	.
Vaccinium vitis-idaea	x	A	A	.	.	.	.	.	.	.	.	.
GRAMINOIDS												
Agropyron latiglume	.	A	.	A	x	x	x	.	x	.	.	.
Agrostis borealis	x	.	.	.	.	.	.	.	.	.	.	.
Bromus inermis	.	.	.	.	.	.	x	.	.	.	.	.
Calamagrostis montanensis	.	.	.	.	x	.	x	.	.	.	.	.
Calamagrostis purpurascens	.	.	.	.	x	.	.	.	.	.	x	x
Carex albonigra	.	.	x	.	x	.	x	.	x	.	x	.
Carex atrata	.	.	.	x	.	x	x	.	x	.	.	.
Carex lugens	x	.	.	.	.	.	.	.	.	.	.	.
Carex nardina	.	x	.	.	.	x	.	x	x	x	x	.
Carex phaeocephala	.	.	.	.	.	x	x	.	.	.	x	.
Carex rossii	.	.	.	x	.	.	.	.	.	.	.	.
Carex rupestris	.	.	.	.	x	.	x	.	A	.	.	A
Carex scirpoidea	.	.	.	.	.	x	x	.	.	x	x	.
Carex scopulorum	.	.	.	.	.	.	.	.	.	x	.	.
Carex spectabilis	x	.	.	.	.	.	.	.	x	.	.	.
C. spp.	.	A	.	.	x	.	.	.	.	.	.	.
Danthonia intermedia	.	.	.	x	.	.	.	.	.	.	.	.
Deschampsia elongata	.	.	.	.	.	.	x	.	.	.	.	.
Festuca altaica	x	.	.	.	.	.	.	.	.	.	.	.
Festuca ovina s.l.[1]	.	A	x	x	x	x	x	x	x	x	A	x
Festuca vivipara	.	.	.	.	.	.	.	.	.	x	.	.
Hierochloe alpina	x	.	x	.	.	.	.	.	.	.	.	.
Kobresia bellardii	.	A	.	.	A	.	A	.	.	A	.	.
Luzula arcuata	x	.	.	.	.	.	.	.	.	.	.	.
Luzula parviflora	x	.	.	.	.	.	.	.	.	.	.	.
Luzula spicata	.	.	x	.	x	x	x	x	x	x	x	.
Oryzopsis exigua	.	.	.	.	.	.	.	.	.	.	x	.
Poa alpina	.	x	.	x	x	x	x	.	x	x	.	.

TABLE 53 (cont'd)

STAND NO.	1	2	3	4	5	6	7	8	9	10	11	12
Poa arctica/grayana	.	x	x	.	x	.	x	x	x	.	.	.
Poa cusickii	.	.	.	.	.	x	.	.	x	.	.	.
Poa juncifolia	.	.	.	.	.	.	x	.	.	.	.	.
Poa palustris	.	.	.	x	.	.	.	.	.	.	.	.
Poa pattersonii	.	.	.	.	x	.	x	.	.	x	.	.
Poa rupicola	.	.	.	.	x	.	.	.	.	.	.	.
Poa sandbergii	.	.	.	.	.	.	.	.	x	.	x	.
Trisetum spicatum	.	.	x	x	x	x	x	.	x	x	x	x
FORBS												
Achillea millefolium	.	.	.	.	.	.	.	.	x	.	.	.
Agoseris glauca	.	.	.	.	x	.	.	x	x	.	.	.
Allium cernuum	.	.	.	.	.	.	.	.	x	.	.	.
Androsace lehmanniana	x	.	.	.	x	.	x	.	x	.	.	.
Androsace septentrionalis	.	.	x	.	x	x	x	.	x	.	x	.
Anemone drummondii	x	x	.	x	x	x	x	x	x	.	x	.
Anemone multifida	.	.	.	.	.	.	.	.	.	x	.	.
Anemone parviflora	.	.	.	x	x	x	x	.	.	.	.	.
Antennaria alpina/umbrinella	.	x	x	x	x	x	x	x	x	x	x	.
Antennaria friesiana	x	.	.	.	.	.	.	.	.	.	.	.
Antennaria rosea	.	.	.	x	.	.	.	.	.	.	.	.
Aquilegia flavescens	.	.	.	.	.	x	.	.	.	.	.	.
Aquilegia jonesii	.	.	.	.	.	.	.	.	x	x	.	.
Arabis drummondii	.	.	.	x	.	.	.	.	.	.	.	.
Arabis lyallii	.	.	.	.	.	.	.	.	.	.	x	.
Arenaria arctica	x	.	.	.	.	.	.	.	.	.	.	.
Arenaria capillaris	.	.	.	.	.	.	x	.	.	.	x	.
Arenaria congesta	.	.	.	.	.	.	.	.	.	x	.	.
Arenaria fendleri	.	.	.	.	.	.	.	.	.	.	.	x
Arenaria macrocarpa	x	.	.	.	.	.	.	.	.	.	.	.
Arenaria macrophylla	.	.	.	.	.	.	.	.	.	x	.	.
Arenaria nuttallii	.	.	.	.	.	.	x	.	x	.	.	.
Arenaria obtusiloba	.	x	x	x	x	x	x	x	A	x	A	x
Arenaria rossii	x	x	.	.	x	.	x	x	.	x	.	.
Arenaria rubella	.	.	x	.	x	x	x	.	x	x	x	.
Armeria maritima	x	.	.	.	.	.	.	.	.	.	.	.
Arnica alpina	.	x	.	.	x	.	x	x	.	x	.	.
Arnica latifolia	.	.	.	x	x	x	.	x	.	.	.	.
Arnica louiseana	x	.	x	.	.	.	.	.	.	.	.	.
Artemisia norvegica	x	x	x	.	.	.	.	.	.	.	.	.
Artemisia pattersonii	.	.	.	.	.	.	.	.	.	.	.	x
Artemisia scopulorum	.	.	.	.	.	.	.	.	.	.	.	x
Aster sibiricus	.	.	.	.	.	x	x	.	x	.	.	.
Astragalus aboriginum	.	.	.	.	x	.	.	.	.	.	.	.
Astragalus alpinus	.	.	.	x	.	x	x	.	x	x	.	.
Astragalus bourgovii	.	.	.	.	.	.	.	x	.	.	.	.
Astragalus umbellatus	x	.	.	.	.	.	.	.	.	.	.	.
Astragalus vexilliflexus	.	.	.	.	.	.	.	.	x	.	.	.
Besseya wyomingensis	.	.	.	.	.	.	.	.	x	.	.	.
Bupleurum americanum	.	.	.	.	.	.	.	.	.	x	.	.
Campanula lasiocarpa	x	A	x	.	.	.	.	.	.	.	.	.
Campanula rotundifolia	.	.	.	.	.	.	x	.	.	.	.	.
Campanula uniflora	x	A	.	.	.	.	.	.	.	.	.	.
Cardamine purpurea	x	.	.	.	.	.	.	.	.	.	.	.
Castilleja flava	.	.	.	.	.	.	.	.	.	x	.	x
Castilleja occidentalis	.	.	x	.	x	x	x	.	x	.	.	.
Cerastium beeringianum	x	.	.	.	x	x	x	x	x	x	.	.
Douglasia montana	.	.	.	.	.	.	.	.	x	.	.	.
Draba incerta	.	x	x	.	.	.	x	.	x	.	x	.
Draba lanceolata	.	.	.	x	x	.	.	.	.	.	.	.
Draba lonchocarpa	.	x	x	.	x	x	x	.	.	.	x	.
Draba oligosperma	.	.	.	.	x							
Draba paysonii	.	.	.	.	x	.	.	.	x	.	x	.
Draba streptocarpa	.	.	.	.	.	.	.	.	.	.	.	x
Epilobium angustifolium	.	.	.	x	.	.	.	.	.	.	.	.
Erigeron aureus	.	.	.	x	x	x	x	.	.	.	x	.
Erigeron compositus	.	.	.	.	.	.	.	.	x	.	x	.
Erigeron peregrinus	.	.	.	x	.	.	.	.	.	.	.	.
Erigeron simplex	.	.	.	.	.	.	.	.	.	x	.	x
Erigeron sp.	.	.	.	.	.	.	x	.	.	.	.	.
Eritrichium argenteum	.	.	.	.	.	.	.	.	.	.	.	x
Fragaria virginiana	.	.	.	x	.	.	.	.	.	.	.	.
Galium boreale	.	.	.	.	.	.	.	.	x	.	.	.
Gentiana amarella	.	.	.	.	x	x	x	.	.	.	.	.

TABLE 53 (cont'd)

STAND NO.	1	2	3	4	5	6	7	8	9	10	11	12
Gentiana glauca	•	•	x	•	•	•	•	•	•	•	•	•
Gentiana propinqua	•	x	•	x	x	•	x	•	•	•	•	•
Gentiana prostrata	•	x	•	•	•	•	x	•	•	x	•	•
Geum rossii	•	•	•	•	•	•	•	•	•	•	•	x
Haplopappus lyallii	•	•	•	•	x	•	x	•	•	•	x	•
Hedysarum alpinum	x	•	•	•	x	x	•	•	•	•	•	•
Hedysarum boreale	•	•	•	x	x	•	•	•	•	•	•	•
Hedysarum sulphurescens	•	•	•	•	x	x	A	A	x	A	•	•
Hymenoxys acaulis	•	•	•	•	•	•	•	•	•	•	•	x
Lagotis glauca	x	•	•	•	•	•	•	•	•	•	•	•
Lloydia serotina	•	•	•	•	•	•	•	•	•	x	•	•
Lupinus lepidus	•	•	•	•	•	•	•	•	•	•	A	•
Lychnis apetala	•	•	•	•	•	x	•	•	•	x	•	•
Lycopodium annotinum	•	•	•	x	•	•	•	•	•	•	•	•
Myosotis sylvatica	•	x	•	•	x	•	x	x	x	x	•	•
Oxyria digyna	•	•	•	•	•	•	•	•	•	x	•	•
Oxytropis campestris/sericea	•	x	x	•	x	•	•	x	x	x	x	•
Oxytropis deflexa	•	•	•	•	•	•	x	•	•	•	•	•
Oxytropis nigrescens	x	•	•	•	•	•	•	•	•	•	•	•
Oxytropis podocarpa	•	A	x	•	A	•	x	•	•	•	•	•
Papaver macounii	x	•	•	•	•	•	•	•	•	•	•	•
Paronychia pulvinata	•	•	•	•	•	•	•	•	•	•	•	x
Parrya nudicaulis	x	•	•	•	•	•	•	•	•	•	•	•
Pedicularis arctica	•	•	x	•	•	•	•	•	•	•	•	•
Pedicularis bracteosa	•	•	•	x	•	•	•	•	•	•	•	•
Pedicularis capitata	x	•	•	•	•	•	•	•	•	•	•	•
Pedicularis groenlandica	•	•	•	•	•	•	•	•	•	x	•	•
Pedicularis lanata	x	x	•	•	•	•	•	•	•	•	•	•
Phlox caespitosa	•	•	•	•	•	•	•	•	•	•	•	x
Phlox sibirica	A	•	•	•	•	•	•	•	•	•	•	•
Pinguicula vulgaris	x	•	•	•	•	•	•	•	•	•	•	•
Polemonium elegans	•	•	•	•	•	•	•	•	•	•	x	•
Polemonium pulcherrimum	•	•	•	•	•	•	•	x	•	•	x	•
Polemonium viscosum	•	•	•	•	•	•	•	x	x	•	•	•
Polygonum bistortoides	x	•	•	•	•	•	•	x	•	x	•	•
Polygonum viviparum	•	A	x	•	A	x	x	x	x	A	•	x
Potentilla diversifolia	•	x	•	x	x	x	A	x	x	x	x	•
Potentilla gracilis	•	•	•	•	•	•	x	•	•	•	•	•
Potentilla nivea	•	A	x	x	x	•	x	•	A	x	•	•
Potentilla uniflora	x	•	•	•	•	•	•	•	•	•	•	•
Potentilla vahliana	x	•	•	•	•	•	•	•	•	•	•	•
Primula angustifolia	•	•	•	•	•	•	•	•	•	•	•	x
Primula egalikensis	x	•	•	•	•	•	•	•	•	•	•	•
Ranunculus eschscholtzii	•	•	•	•	•	•	•	•	x	•	•	•
Romanzoffia sitchensis	•	•	•	•	•	•	•	•	x	•	•	•
Rumex acetosa	x	•	•	•	•	•	•	•	•	•	•	•
Saussurea densa	•	•	x	•	x	x	x	•	•	•	•	•
Saxifraga bronchialis	•	•	x	x	x	x	•	A	x	•	x	•
Saxifraga caespitosa	•	•	•	•	x	•	x	•	•	•	•	•
Saxifraga cernua	•	x	•	•	x	•	x	•	•	•	•	•
Saxifraga flagellaris	x	•	•	•	•	•	•	•	•	•	•	•
Saxifraga occidentalis	•	•	•	•	•	x	x	x	x	•	•	•
Saxifraga oppositifolia	x	A	•	•	•	x	x	x	x	•	•	•
Sedum lanceolatum	•	•	x	x	x	x	x	x	x	•	x	x
Sedum roseum	•	•	•	•	•	•	x	•	x	x	•	•
Selaginella densa	•	A	x	x	x	x	A	x	x	x	x	x
Senecio canus	•	•	•	•	•	•	•	•	•	x	•	•
Senecio conterminus	•	•	•	•	•	•	•	x	x	•	•	•
Senecio lugens	•	•	•	•	x	•	x	•	•	•	•	•
Senecio werneriaefolius	•	•	•	•	•	•	•	•	•	x	•	•
Silene acaulis	A	A	x	x	x	x	x	x	x	x	x	x
Silene parryi	•	•	•	•	•	•	•	•	•	x	•	•
Smelowskia calycina	•	•	•	•	A	•	x	A	A	x	•	•
Smelowskia ovalis	•	•	•	•	•	•	•	•	•	•	x	•
Solidago multiradiata	•	•	x	A	x	x	•	x	x	x	x	•
Stellaria longipes	•	x	•	x	x	•	x	x	x	•	•	•
Taraxacum lyratum/ceratophorum	•	•	•	x	x	x	x	•	•	•	x	•
Thalictrum alpinum	x	•	•	•	•	•	•	•	•	•	•	•
Tofieldia coccinea	x	•	•	•	•	•	•	•	•	•	•	•
Tofieldia pusilla	x	•	•	•	•	•	•	•	•	•	•	•
Trifolium dasyphyllum	•	•	•	•	•	•	•	•	•	•	•	x
Woodsia glabella	x	•	•	•	•	•	•	•	•	•	•	•
Zigadenus elegans	x	•	•	•	x	•	•	x	x	•	•	•

NOTE: A>1% cover, x<1% cover.

[1]Includes F. baffinensis, F. brachyphylla, F. ovina.

TABLE 53 (cont'd)

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1. *Dryas octopetala*-lichen community, Nome, Alaska; 2 stands (Hanson 1951, 1953).
2. *Dryas*-lichen community, Signal Mt., Jasper N.P., Alberta (Hrapko 1970).
3. *Dryas octopetala*/lichen community type, Bald Hills, Jasper N.P., Alberta; 5 stands + unsampled stands.
4. *Dryas octopetala-Empetrum nigrum* association, Bow Summit, Banff N.P., Alberta; 7 stands (Broad 1973).
5. *Dryas hookeriana-Oxytropis podocarpa-Cetraria cucullata-C. nivalis* association, Snow Creek Valley, Banff N.P., Alberta; 5 stands (Beder 1967).
6. *Dryas octopetala*/lichen community type, Yoho N.P., British Columbia (P. Kuchar, unpublished).
7. *Dryas octopetala* association, Highwood Pass, Alberta; 7 stands (Trottier 1972).
8. *Dryas* tundra, S of Bovin L., Crowsnest Forest Reserve, Alberta (Kuchar 1973).
9. *Dryas* tundra, Waterton Lakes N.P., Alberta; 2 stands (Kuchar 1973).
10. *Dryas octopetala* tundra, Siyeh Pass, Glacier N.P., Montana; 16 stands (Bamberg and Major 1968).
11. *Dryas octopetala* community, North Cascades, Washington - B.C.; 10 stands (Douglas 1973).
12. Dryasetum octopetalae, Longs Peak, Colorado; 6 stands (Kiener 1967).

(e.g. Holway and Ward 1965, Beder 1967, Kuramoto and Bliss 1970, Broad 1973). Vegetation in the Bald Hills can be correlated with snowcover (Fig. 13, Table 24): thin snowcover in the Stony Tundra Group, moderately deep cover in the Heath Group, deep cover in the Snowbed Group, moderate cover and upslope snowbanks in the Herb Meadow Group.

The order of snow-release of major plant communities in the Bald Hills is the same as that reported by Hrapko (1970) for tundra communities on Signal Mountain. Major phenological events occur first in upland tundra communities, then in heaths and finally in snowbeds. Herb meadows have a long phenosequence and in this and other ways may not be true, i.e. "zonal" (Chernov 1971) tundra communities.

"Temperature is often emphasiaed as being the most important ecological factor in the tundra, controlling growth and development of the plants" (Rønning 1969). Soil and surface temperatures are highest in Stony Tundra, lowest in Heaths, and intermediate in Herb Meadow and Snowbed communities. After snowmelt, temperatures rise and % soil moisture falls in the *Carex nigricans* snowbed community (Fig. 16). Soil drought is accentuated in later-release sites because of the relative lack of meltwater, relatively high evapotranspiration, and rocky soils low in humus and water-retaining capacity (Billings and Bliss 1959).

Other factors, e.g. aspect, windspeed, elevation, are less well correlated with community types; most can be traced to the basic correlation with depth and duration of snowcover.

Correlation with bedrock, an important independent variable, is generally too low to be of value. Correlation with soils is also fairly poor; however, there is generally better profile development under mesic conditions, good plant cover, and at least some snowcover. Brunisols are mainly under heath cover, Gleysols in bogs, and Regosols in most other communities.

Species richness

In the *Dryas*/lichen to *Carex nigricans* transect (Table 23) species richness per unit area is highest in the sections dominated by *Cassiope tetragona* and *Phyllodoce glanduliflora*, slightly lower in the *C. mertensiana*, *Luetkea pectinata* and *Dryas octopetala* sections, and very low in the *Carex nigricans* snowbed. Relative numbers of lichen, bryophyte and vascular plant species is ca. 3:2:4 in the heath communities. There are many fewer vascular plant species in the *D. octopetala*/lichen segment, but many more lichens.

Species richness in heath communities is relatively high despite the relatively dense dwarf shrub layer. Although the heaths tend to homogenize the habitat, there are enough microsites, viz. small deflation patches, eroding dead heath clumps, and micro-hummocks and hollows to allow a variety of plants to maintain themselves. Their low cover (Table 17), however, reflects the competitive dominance of *Cassiope* and *Phyllodoce*.

Species richness can be highest in the habitats most favorable for plant growth, and lowest (or nil) in the most

unfavorable (Whittaker 1965, Benninghoff 1968). In the Bald Hills, high numbers of vascular plant species in mesic habitats viz. heath communities and herb meadows, and low numbers at both the snowfree and snowbed ends of the habitat spectrum, conform with the notion that the most severe alpine environments are late-lying snowbeds and dry windswept ridges (Billings and Mooney 1968). These authors further note that in both cases cryptogams characterize the limits of plant growth, usually mosses in snowbanks and crustose lichens on ridges.

The opposite view was elaborated by Douglas (1973) in his investigations of alpine communities in the N Cascades. He classified snowbed communities as mild environments, noted relatively few species in them, and consequently concluded that species richness was low in mild environments and high in fairly harsh environments.

Succession

In their important review of dynamic concepts in tundra vegetation, Churchill and Hanson (1958) present the argument: "The principal reason for questioning the applicability of a climax concept to arctic and alpine areas is concerned with the apparent instability of the habitat and vegetation." Part of their conclusion, however, is that "The permanence of many communities in arctic and alpine areas indicates that changes in the habitat are not significant or that the species present in rapidly changing habitats, such as solifluction areas, are adapted to them."

Dynamic concepts have played a very minor role in elucidating the mosaic of tundra communities, compared to environmental correlations especially with soil moisture. Attempts to invoke successional relationships have had much less success in arctic and alpine tundra vegetation than in forest ecosystems. For example, Drury (1962) found the concept of succession of little value in describing the vegetation of Bylot Island. In Utah alpine tundra, Hayward (1952) saw "a complex of community development that is most confusing to the ecologist who attempts to gain some comprehension of the successional processes in operation."

Most tundra communities in the Bald Hills can be considered in a climax state. Except for rockfalls, rockslides, and man-disturbed surface at the N end, the vegetation mosaic is probably stable. Autogenic succession, i.e. the short-term, organism-induced unidirectional replacement of entire communities, would be an incorrect view of the history or ultimate fate of most of the communities. There is an exceedingly slow process of allogenic succession, due mainly to gradual infilling of basins (cf. Hayward 1952, Douglas 1972). The only short-term dynamic phenomena are cyclical, e.g. the buildup and degradation of hummocks, or very slow spread and erosion of *Dryas* mats.

ECOLOGY OF *DRYAS OCTOPETALA*

Ecological dynamics of *D. octopetala*

Dryas octopetala is the outstanding dominant of drier alpine tundra communities in the Bald Hills, and probably the most important plant species in the alpine zone of the Canadian Rockies. In some communities it comprises up to 99% of the plant cover. In others it may have only 1-10% live cover, but by virtue of its mat habit provides the chief amelioration of microhabitat. On Signal Mt., Hrapko (1970) noted that "wherever *Dryas* occurs it is usually the primary or occasionally the secondary dominant; this can be said of no other alpine species."

D. octopetala is *alpha* and *omega* in community dynamics. It is firstly a colonizer: because *Dryas* occupies shallow stony soils showing minimal profile development, it is often considered pioneer, paving the way for later invaders especially certain graminoids. *D. octopetala* may simultaneously be part of an apparently stable community type evincing no shifts in composition or dominants. Both views, at first glance contradictory, are supported by some authors.

Working in the Pyrenees, Braun-Blanquet (1948) argued that ordinarily the progression from *Dryas octopetala* to *Kobresia bellardii* was only a matter of time. This view of *D. octopetala* as a seral species in Europe is supported by Elkington (1971).

Cox (1933), diagramming his concepts of alpine climax in Colorado, indicated both the xerose (including *Dryas*-

dominated communities) and hydrose trending toward alpine meadow climax, the Elynetum. However, he concluded that "The Dryas association forms an edaphic climax on the exposed slopes and appears destined to persist as long as the conditions of wind, snow duration, and rocky soil remain as they are at present."

Kiener (1967) stated: "As a pioneer plant, *Dryas octopetala* has a world wide reputation." In Colorado he noted that "The Dryasetum is a pioneer association in the sense of being able to invade a bare area." Nevertheless, the *Dryas* association that he described had all appearances of stability, and no indication was given as to what if anything might succeed it.

In Utah, Hayward (1952) considered the true alpine climax, dominated by sedges and grasses, to be restricted to relatively flat tops of high ridges. In his opinion subclimax communities occupied upland sites in glacial valleys and included a variety of grasses, sedges, forbs, and also *Dryas octopetala*. By this outdated topographic-based view of climax, these communities might never reach the climax condition.

In southern Alberta, Bryant and Scheinberg (1970) reconstructed a successional sequence from lichen tundra through *Dryas octopetala* cover to a climax community dominated by *Carex nardina* and *Selaginella densa*. Although *Dryas*-dominated vegetation is here viewed as a seral stage, the authors concluded that due to disruption by frost and

wind erosion, a cyclical state exists and climax vegetation in the traditional sense will not be reached.

In an alpine site in Banff Park, Broad (1973) noted numerous *Picea* and *Abies* seedlings in *D. octopetala* cover, and considered this evidence of succession to *Picea-Abies/Phyllodoce*. But he opined that tree establishment was retarded by mechanical disturbance and wind erosion of organic matter and upper soil horizons.

Perhaps most confusing are Oosting's (1948) views on vegetation in Greenland. Solidly entrenched as he was in the mainstream of North American dynamic ecology, Oosting did not fail to note that previous studies of Greenland's vegetation had been floristic or community-descriptive and that suggestions of successional relationships appeared only rarely. He found *Dryas octopetala* dominant over extensive areas, but postulated an ericaceous heath climax for the region. He noted that successional relationships were "complicated by the appearance of the major species in almost every locality and under varying conditions. Frequently climax species may appear as pioneers and numerous pioneer species are always abundant in every climax community." But he also realized that "Evidence that succession on the xeric sites proceeds eventually to the climax is not available." Oosting seems to have ascribed successional status to vegetation that was in all likelihood a climax type.

The consensus of viewpoints is, then, that *Dryas octopetala* is a *bona fide* pioneer species, that it has seral

attributes, but that it is usually not succeeded due to insufficiently altered habitat. A rather different view of *Dryas*-dominated vegetation, probably more realistic than the seral-climax idea, is that of the cyclical climax (Churchill and Hanson 1958). This notion of vegetation as a mosaic of chronologically related units, i.e. a regeneration complex (Watt 1947), obviates the need (in some vegetation types) for concepts such as "climax" and "seral".

In northern Norway, Coombe and White (1951) described a regeneration complex in which "The patches which constitute the community as a whole can be classified into five phases, which are spatially distributed to form a mosaic pattern... and seem to bear a temporal relationship to one another which is cyclical, the end of the last phase being very similar to the beginning of the first." Phase one had many species intolerant of competition, among them *Dryas octopetala*. Phase two had a closed plant cover dominated by *Carex rupestris*, *D. octopetala* and *Empetrum hermaphroditum*, on 5 cm of peat. By the time 15 cm of peat had accumulated, few of the original species remained. A few weak shoots of *D. octopetala* persisted. Lichens were abundant in phase four. Phase five involved peat erosion down to mineral surface.

In Iceland, Anderson (1967) described a regeneration complex with *Dryas octopetala* playing the central role. It was the chief colonizer of eroded sites. In the next phase, *Kobresia bellardii* rooted in the decaying centres of *Dryas* clones. Phases three and four were characterized by the

dominance of *Betula nana* and *B. pubescens* respectively. Eventual erosion allowed re-invasion by *Dryas* and the start of a new cycle.

Dryas-heath vegetation such as described by Coombe and White (1951) and Anderson (1967) is not found in the Bald Hills (and probably not in the Canadian Rockies in general). Furthermore, in much of the *Dryas*-dominated vegetation there is no evidence for a mosaic-type successional sequence in which *D. octopetala* invades, is replaced by other plants, and re-invades. The nearest thing to such a sequence occurs in *Dryas* matfields, where mats are colonized by varicus plants, undergo fragmentation, and rejuvenate.

Vegetation dominated by *Dryas octopetala* seems much less prone to change in the Canadian Rockies than in the southern Rockies or central Europe. Throughout the Rockies, the species was probably an important colonizer following deglaciation. In the southern Rockies (and central Europe) it is at present severely limited in area, therefore its role as a seral species might once have been very important. In the Canadian Rockies however, it is presently the dominant of meso-xeric tundra. It is theoretically possible that most of this *Dryas*-dominated tundra will eventually be replaced by a graminoid climax dominated chiefly by *Kobresia bellardii* (Cox 1933) or by *Carex nardina* (Bryant and Scheinberg 1970). This sequence, were it to occur at all, would take hundreds or more likely thousands of years. In the Bald Hills these "climax" graminoids are presently restricted to small sites,

chiefly certain S-facing slopes and ridge crests. Only these offer the combination of relatively stable site that does not dry out excessively in summer yet remains virtually snowfree all year (cf. Bell 1974).

So, in contrast to central-latitudes *Dryas octopetala* which may be seral, and its low-altitude relative *D. drummondii* which is strictly seral over its entire range, the Canadian Rockies *D. octopetala* is a *bona fide* climax species. In many upland alpine sites it forms part of a very characteristic and long-lived ecosystem rich in lichens, and harboring a predictable assemblage of vascular plants and arthropods.

This same latitudinal shift from seral to climax role is seen in other plant species, e.g. *Picea glauca*. In the transition zone between boreal and eastern deciduous forest, *P. glauca* is a seral species common in disturbed sites. Northward it is increasingly more "climax", and in the boreal forest is a climax dominant (G.H. La Roi, *pers. comm.*).

<u>Threats to *Dryas octopetala*</u>

Physical environment

Since *Dryas octopetala* does not lay down a continuous litter layer as do heaths, it is vulnerable to deflation through needle-ice formation. Washburn (1969) considers this phenomenon extremely important in the Arctic, where the frequency of freeze-thaw cycles is evidently much lower than in the Bald Hills. But much of the *Dryas* vegetation in the Bald Hills occupies gravelly uplands where needle-ice

formation is thwarted by lack of surface fines and moisture. In *D. octopetala/Polytrichum piliferum* communities, deflation probably accounts for the incomplete *Dryas* cover. The mats seem to be eroded slowly enough that they can continue to colonize recently denuded or cryptogam-stabilized segments of the surface, and thus maintain a significant mat population and cover.

A key to *Dryas'* success may be its partial but not total alteration of the ground surface. Total stabilization allows species such as *Carex nardina, Selaginella densa* and *Cetraria cucullata* to colonize *Dryas* mats and eventually totally exclude them (Bryant and Scheinberg 1970). The strategy of *Dryas* is to gain a sufficiently strong foothold and stabilize the surface enough to preclude rapid erosion, but at the same time alter the edaphotope so little that other plants have difficulty in establishing or maintaining themselves. Wind is helpful in breaking up senescing mats harboring many vasculars and cryptogams, into "clean", physiologically rejuvenated clones.

Drought does not appear a serious problem for *Dryas octopetala* in the Bald Hills. It has circumvented late-season drought by completing most growth in the early part of the season, mostly May-June (Fig. 20), when soil moisture levels are still adequate (Fig. 16). *D. integrifolia* in the Arctic has a high resistance to water loss (Addison 1973, Svoboda 1974), mainly due to the tomentose lower epidermis of the leaf (Addison 1973). The prostrate habit has obvious

adaptive significance in windy uplands. However, the absence of *D. octopetala* on snowfree tops of solifluction terracettes may be due to abrasive or desiccating action of wind (cf. Billings and Mooney 1968).

D. octopetala mat form varies widely, an expression of specific environmental conditions. Leaf size varies as a function of site, the warmest sites generally with largest-leaved plants, and mats on windy ridges with smallest leaves. Svoboda (1974) opined that reduced leaf area is part of the survival strategy in xeric polar habitats, by exposing a smaller transpiratory surface, and by curbing excessive heating.

On Devon Island, Addison (1973) reported *Dryas integrifolia* leaf temperatures above 46°C for a 3-hour stretch, with no signs of heat kill. Svoboda (1974) found most *D. integrifolia* leaves oriented so as to substantially lower direct exposure to the sun. He speculated that direct exposure would probably lead to intolerable temperature rises. Whereas *D. integrifolia* with its cushion habit may be unable to dissipate energy effectively, *D. octopetala* with its looser mat form will probably not experience as high temperatures.

Continually high temperatures may be lethal to *D. octopetala* by creating exorbitant respiratory demands. This may be the reason why transplants that I kept in Edmonton died. Whereas *Dryas integrifolia* and *D. drummondii* occur well into the montane zone (to ca. 1100 m) in the Canadian

Rockies, *D. octopetala* seems confined to the alpine and subalpine zones (down to ca. 1650 m). In Colorado it is found mostly on N-facing alpine slopes (Kiener 1967, Benedict 1970).

In the High Arctic, the distribution of *D. integrifolia* may be at least partly governed by minimum, not maximum, heat. In the western Queen Elizabeth Islands, Babb and Bliss (1974) found it restricted to warmer sites.

Seasonal and annual weather vagaries are overcome by *Dryas'* "opportunism". *D. octopetala* can tolerate from virtually snowfree to rather late snow-release conditions. According to Mayo et al. (1973), *D. integrifolia* "appears to be well adapted to take advantage of almost any conditions experienced during the growing season and assimilates CO_2 for some portion of the day." Svoboda (1974) recorded positive photosynthetic balance in *D. integrifolia* at leaf temperatures of 3-4^{o}C.

Biotic environment

1. Competition.

On the subject of High Arctic habitats with very low plant cover, Savile (1960) noted: "Under such severe physical restrictions biological competition is greatly reduced and is often negligible. In warmer arid lands a sparse ground cover is often accompanied by an extensive root system, and the ground may thus be nearly fully occupied. But in these arctic deserts the root systems generally occupy approximately the same area as the aerial parts of the plants."

Benninghoff (1968) remarked that "The high latitude environments impose intense physical stresses and relatively weak biotic environmental stresses."

In its "nodal" habitat, *Dryas octopetala* does not seem competitively threatened by any plant species. Most other vasculars form small, widely spaced slones, and there is virtually no shading. *Dryas* mat cover is frequently greater than that of all other species combined. Bryophytes do not infringe on *Dryas'* growth because the habitat disallows development of large, thick moss masses. Lichens are lower instature than *Dryas*, and none are epiphytic on living leaves. Potential competition might come from mat analogues especially *Salix arctica*, but it does not do well in most upland tundra. *Empetrum nigrum* is rarely abundant and seems to occupy the most mesic microsites (cf. Hrapko 1970).

Dryas' natural ecological amplitude terminates in the *Cassiope tetragona/D octopetala* community. Communities that are more mesic have few, doubtless temporary *Dryas* clones that seem able to invade only by seed. The environmental conditions here may be quite adequate, possibly ideal, for the growth of *D. octopetala*: vigorous mats can be found on recently denuded heath tundra surfaces. Low competitive ability is doubtless the primary reason for *Dryas'* abysmally poor showing in mesic alpine habitats. Although it is an outstanding colonizer and can at the outset spread more rapidly than heaths (Fig. 23), these (in Heath Tundra) or herbs (in Herb Meadows) eventually form a dense cover and

exclude it. Studies in Europe (Coombe and White 1951, Anderson 1967) demonstrate that the development of a heath or other shrub cover relegates *Dryas octopetala* to a minor position or eliminates it entirely.

2. Disease.

In the study area *Dryas octopetala* had a very low incidence of disease symptoms. Most of the fungal species recorded on it from the Arctic (Conners 1967) seem to be saprophytes of the dead leaves. In marginal situations, e.g. excessively damp or shaded, the plant does seem susceptible to attack by pathogens. This may be a further reason why *D. octopetala* is generally absent from mesic or meso-hydric tundra.

3. Herbivores.

Very few animals eat live *Dryas octopetala*. Noctuid larvae attack its least important part, the floral tissue. Most reproduction by *Dryas* seems vegetative, disparaging the value of flowers. *Nepticula* moths whose larvae might mine *D. octopetala* leaves, were commonly seen at the flowers. But incidence of leaf mines was very low, seemingly restricted to unusual sites e.g. under krummholz.

Two important *Dryas* herbivores in the Bald Hills, *Eotetranychus* sp. and *Chorizococcus* sp., were consistently associated with the plant. I do not know what sort of population levels would be required for serious debilitating effects on the plant, or what their regulatory mechanisms

are. The Tetranychidae include some notorious economic pests of worldwide significance. The total life cycle of *Tetranychus urticae*, the glasshouse red spider mite, requires as little as 19 days (Mitchell 1973). However, females and young feed in a restricted area of the leaf and exhibit little activity if they are not crowded and resources are abundant. *Eotetranychus* sp. was not found in high numbers on any *Dryas* plants or leaves.

White-tailed ptarmigan are probably the only vertebrate at least partially dependent on *D. octopetala* for food in the Bald Hills. In arctic and alpine areas ptarmigan utilize *Dryas* leaves mainly in spring and fall (Gelting 1937, Aleksandrova 1964, West and Meng 1966, May and Braun 1972). The plant seems to have very little direct significance in the maintenance of other tundra vertebrate populations in the Bald Hills. The animals are all attracted to the general habitat - the xeric, open and/or rocky tundra - rather than to particular plant species.

I do not know the overall effect of herbivores on the economy of *Dryas octopetala* in the Bald Hills. Heavy infestations by *Chorizococcus* or *Eotetranychus* might explain the death or poor health of some mats. But this was not investigated and is purely conjectural.

<u>Effects of *Dryas octopetala* on associated biota</u>

The direct relationship of *D. octopetala* to plants and animals in the Bald Hills is diagrammed in Fig. 34. The plant is important to many species as a direct or

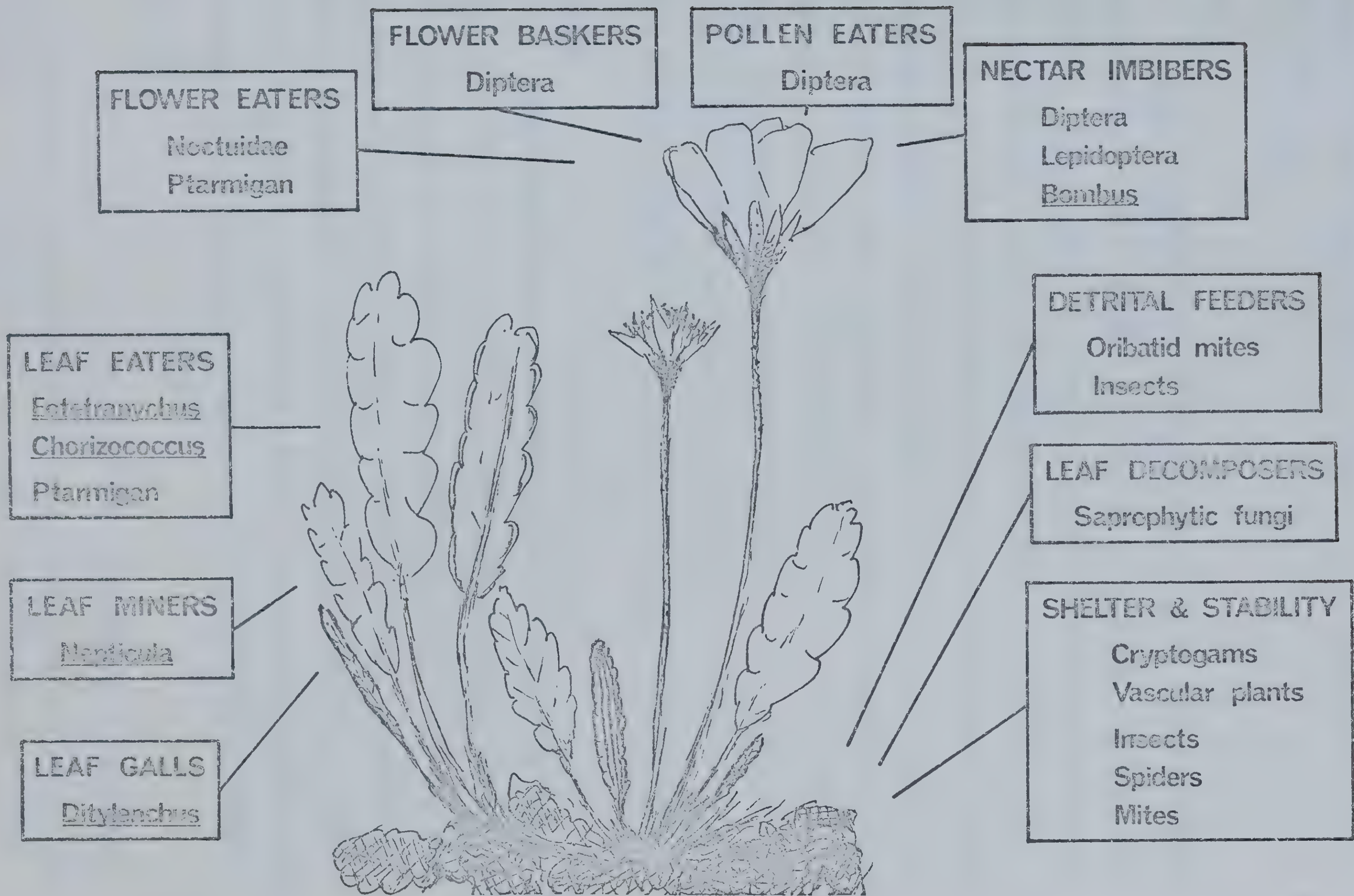

FIG. 34. Diagram of first-order relationships of biota to *Dryas octopetala* in the Bald Hills.

indirect food source, and as a microsite of relative warmth and stability.

Food

Many insects feed on *Dryas* nectar and pollen (Hocking 1968, Kevan 1970). Simply by virtue of its high cover and biomass, *Dryas* might be critical to the continued existence of populations of many of these in upland alpine habitats. *Dryas* seems especially important early in the season, but as forb-rich meadows and heaths come into flower there seems a general insect exodus to these. Excluding nectar and pollen feeders, relatively few herbivores utilize *D. octopetala*. Only two species seem obligate, the others are opportunists, using *Dryas* leaves and flowers when they are available or when other, presumably more palatable, foods are scarce.

Litter

Many arthropods are attracted to the organic matter that *D. octopetala* creates. A food web, based on litter laid down by *Dryas* and plants in the *Dryas* mat, involves a large variety and number of detrital feeders, mainly oribatid mites, together with their predators and parasites. Mats are then loci of arthropod activity, involving a large percentage of all organisms found in *Dryas*-dominated tundra.

Warmth

In daytime *D. octopetala* mats are among the warmest of microsites. Temperatures do not reach the extremes reported for *D. integrifolia* in the High Arctic (Addison 1973,

Mayo et al. 1973), which might be lethal to the generally cold-adapted alpine fauna. But temperatures above ambient are of definite advantage to arthropods, increasing metabolic rate and efficiency. The flowers of *D. integrifolia* are important warm microsites in High Arctic tundra (Kevan 1970).

In terracette *D. octopetala*/lichen communities in the Bald Hills, the warmest microsites are the bare terracette tops and coolest the mossy hollows. Greatest arthropod activity was recorded in the latter (Fig. 32, Table 39). Some factor other than warmth, probably humidity in the boundary layer, is attractive to the animals.

Shelter and stability

Dryas octopetala is a very important ameliorator of microenvironment. Surface and wind movement are dampened within mats. The mats are noda of plant and arthropod populations. In some communities on loose sliding shale or on windswept ridges, most cryptogams and many of the vascular plants are virtually or totally restricted to the centres of *Dryas* mats (e.g. Table 28). Arthropod numbers and activity are much higher in these mat "islands" than outside them (Table 35, Figs. 30,32). A few species, e.g. the collembolan *Entomobrya nivalis* and the phalangid *Leptobunus* sp., seem to shun the mats (Fig. 32, Table 39).

Dryas octopetala may function in nutrient release to associated plants. Svoboda (1974) viewed *D. integrifolia* clumps as micro-ecosystems, absorbing nutrients from very

limited surrounding sources, and probably recycling most of these. *Dryas* species in at least some sites are nitrogen fixers (Tisdale et al. 1966, Lawrence et al. 1967, Elkington 1971), and might thus enhance edaphic resources for other plants. On recently deglaciated terrain *D. drummondii* plays an important role in nitrogen fixation and may accelerate succession to mature forest by 20-30 years (Lawrence et al.). *Dryas octopetala* cannot be nearly so important in substrate amelioration. It has a relatively slow growth-rate (Fig. 22, Table 27) and usually forms an incomplete cover; furthermore, the very fact that it is not succeeded by other plants suggests that the edaphotope is altered very little by it.

Effectiveness of *D. octopetala* in different habitats

The effectiveness of *D. octopetala* as a substrate for plants and arthropods is partly tempered by physical environment. In exposed unstable sites, particularly those with a loose surface, litter accumulation is prevented by wind and by relatively rapid movement of pebbles through mats (cf. Tables 28-30). In Waterton Lakes Park I saw, on some warm-aspect limestone scree slopes in the subalpine zone (1650 m), *D. octopetala* mats that harbored no macroscopic plant life. Mats in such unstable habitats are very poor micro-refugia for biota, and although *Dryas* itself may survive, little else can. At the other extreme, lush *Dryas* mats in some warm but sheltered and mesic sites produce leaves over the entire mat surface, and other plants may be excluded. Arthropod activity and numbers, however, may be enhanced.

High-elevation *D. octopetala*/lichen tundra is floristically and structurally similar to that at lower altitudes, but seems less effective in maintaining an active arthropod fauna (Tables 47,48). In 1972, arthropods were caught in extremely low numbers on bare gravel at the highest elevation (Appendix 11). The large catch discrepancy between bare gravel and *Dryas* mats suggests worse-than-normal environmental conditions in that year, possibly higher wind velocities that would curtail animal activity outside of plant cover. These data suggest that *Dryas* mats may be critical to the continued success of many high-elevation arthropods in years of abnormal environmental stress.

Commensalism between *Dryas octopetala* and associated biota

Dryas octopetala is a boon to a wide range of arthropods and plants in some upland alpine habitats. It is much more important for them than they for it. The only real benefit to *Dryas* is enhanced seed set through pollinator activity, but since most plant reproduction seems vegetative, this is probably not very important for its continued success.

Each *Dryas* mat in upland matfields is a "life support system", providing food, shelter and stability for plants and arthropods. The mats are critical to the maintenance of some cryptogam populations in matfield situations. This is not to imply that dependence is total, for many other sites e.g. fellfields and boulderfields, cliffs, outcrops, support associations of the same cryptogams in the absence of *Dryas*.

Numerous flies and some other insects, e.g. *Nepticula* spp., probably depend on the flowers of *D. octopetala* over all other species' for shelter and warmth and, most importantly, as a food source. Very few arthropod species are demonstrably host-specific on *Dryas*, but populations of many are enhanced and possibly dependent on it for their continued existence in upland tundra habitats.

As a host *D. octopetala* is near-perfect: it is abundant, stable, long-lived, and usually tolerant of plants and animals in the mats. In contrast, mat analogues of *D. octopetala* have much lower cover and importance therefore for plant and arthropod populations. *Silene acaulis* would be an excellent host were its cushions larger and more numerous. *Empetrum nigrum*, on the other hand, supports a relatively depauperate arthropod fauna, and few plants grow in it. Hrapko (1970) noted that the more compact, closed cover of *Empetrum* probably inhibits the establishment of some vascular plants. *Salix arctica* may support a relatively large feeder fauna (Hering 1957, Buhr 1964, Oliver et al. 1964, Kevan 1970), but it does not accumulate litter and therefore has relatively few plant and detrital animal associates.

Dryas octopetala in the Canadian Rockies is evidently a very "clean" plant. Its large biomass and broad range, yet very limited utilization by herbivores, is a perplexing aspect of its ecology. Many arthropods have developed a dependence on *Dryas* flowers for food and warmth, but the vegetative parts of the plant entail a great waste from the standpoint

of potential herbivores. Intensity of use seems very low, reflecting a general trend toward fewer numbers of herbivorous species and overall lesser significance of phytophagy in harsher environments (cf. McAlpine 1964, Oliver et al. 1964).

The low utilization may reflect the presence of biochemical substances in *Dryas* rendering it unpalatable, unpleasant or otherwise unfit for consumption. Two other hypotheses might also be considered:

(1) There has been a slow rate of evolution of *Dryas* phytophagy. Rapidly changing environments due to glaciation, and the general "slowness" of life in tundra habitats, might be two of the more important factors.

(2) Community evolution may have favored the ascendancy of detrital feeders, and conservation of the chief photosynthetic apparatus in upland tundra. *Dryas* may be the key to the upland alpine ecosystem, and heavy attack by herbivores as well as pathogens might imperil the entire system.

In conclusion, *Dryas octopetala* is an eminently successful plant, enjoying a relatively competition-free habitat, low incidence of disease, and low incidence of utilization by herbivores. *Dryas*-dominated communities are generally stable; in most, light to moderate needle-ice and wind action, together with natural senescence and mat fragmentation, result in an incomplete, ever-shifting but never really different cover. In the Canadian Rockies, the inability of *D.*

octopetala to significantly alter the habitat may be the key to its climax status. In upland tundra it is an exemplary ecological dominant, i.e. a species which largely controls the energy flow and strongly affects the environment of all other associated species (Odum 1971). In the shale "balds" in the Bald Hills it creates conditions favorable for the development of many populations of vascular plants, cryptogams, and arthropods. There is a commensal relationship between *Dryas octopetala* and associated biota, *Dryas* neither enhanced nor suppressed, but plant and animal populations greatly benefiting.

10. SUMMARY

1. The Bald Hills study area lies just west of Maligne Lake in Jasper National Park, and entails the alpine and forest-tundra zones of a small range of low mountains, mainly Ordovician shales and conglomerates, that were scoured to rounded hills by Pleistocene glaciers. Timberline is at 2000-2150 m ASL, krummholz reaches 2350 m, and tundra vegetation ascends to the summit at 2600 m.

2. The climate is modified continental. July & Aug mean air temperature 10 cm above ground for 1968-70 at 2300 m was 7.1°C. Maximum air temperature recorded in the Bald Hills was 21°C at the fire lookout (2135 m) and 28°C at 10 cm above a steep S-facing slope; minimum was -27°C. Summer freeze-thaw cycles occurred on ca. 15% of nights in the "balds", but up to 45% in some meadows in the path of cold-air drainage. Summer precipitation ranged from 70-200 mm. Vapor pressure deficits were generally low, averaging 3 mb and rarely exceeding 10 mb. Wind speeds were moderate, averaging less than 2 m/sec at +40 cm. Weather is highly variable through the season and between years.

3. Soils are developed mostly on till, locally on colluvial and alluvial deposits. They have shallow profiles, weak structure, low nitrate and phosphate, very variable potassium, and are medium to very strongly acid. Sandy loams predominate, often with high cobble content. Congeliturbation

has disrupted many profiles. Upland tundra has mostly Orthic Regosol profiles; Cumulic Regosols occur on some steep slopes; Alpine Dystric Brunisols have developed under a complete plant cover, mainly heath tundra; Gleysols are restricted to a few small pockets of impeded drainage.

4. Birds and mammals common in the area are the water pipit, horned lark, gray-crowned rosy finch, white-tailed ptarmigan, Rocky Mountain caribou, Columbian and golden-mantled ground squirrels, pika, mule deer, and shrews.

5. A total of 642 species of arthropods have been collected in the Bald Hills; an estimated 1000 species of invertebrates inhabit the tundra. As in most other tundra areas, both arctic and alpine, the most numerous and diversified arthropods are mites, collembolans, spiders, flies, parasitic hymenopterans and beetles.

6. The flora includes 197 vascular plant species, 118 bryophytes and 137 lichens. It has strong Arctic and Cordilleran affinities, and there are no regional endemics. Vascular species richness compares favorably with that of other North American tundra sites. The relatively high cryptogamic diversity is at least partly attributable to the more intensive collecting.

7. Vegetation was sampled quantitatively in 22 stands, two intensive *Dryas* matfield sites, and five transects. *In situ* observations and ordination helped elucidate 23

community types in four major Groups:

(1) Stony Tundra, on ridges and slopes of all aspects, with little snow accumulation; dominated by mat, cushion and rosette forms, and rich in lichens;

(2) Heath Tundra, mainly on N and E aspects; dominated by *Cassiope mertensiana*, *C. tetragona*, *Phyllodoce glanduliflora*;

(3) Herb Meadows, in mesic to meso-hydric sites; high in vascular plant cover and species richness; *Artemisia norvegica* the binding species;

(4) Snowbeds, with a physiognomically heterogeneous group of community types but having in common very late snow release and a depauperate flora.

8. The mosaic of plant communities is correlated with depth of snowpack and time of release. Stony Tundra communities are typically covered by less than 1 m of snow, and melt out in April-May (unless snowfree essentially all winter); the flowering peak occurs in June. Heath Tundra has snowpack from 0.5 to 3 m or more; it melts out by mid-June and flowering peaks in early to mid-July. Snowbed communities melt out in late June-July. Herb Meadows melt out in early june, and are supplied with meltwater from upslope snowbanks.

9. The phenology of most vascular plant species is dictated by snow-release dates. A few Herb Meadow species (e.g. *Trollius laxus*) begin flowering at the same time each year. In general, the more snow that a community accumulates, the

greater the year-to-year amplitude in onset of plant growth.

10. Bald Hills tundra vegetation is similar to that in many other parts of the Canadian Rockies N of 50°N lat. A few community types described elsewhere do not occur in the study area. Two snowbed community types in the Bald Hills are apparently previously undescribed. Upland arctic tundra has some similarities in structure, composition and hydro-edaphic relationships to Bald Hills tundra. Tundra in the central and southern Rockies, and in central and southern Europe, is rather dissimilar especially structurally.

11. The mat-forming dwarf shrub *Dryas octopetala* ssp. *hookeriana* is the dominant of the *D. octopetala*/lichen community, the nodal community types of Stony Tundra in the Bald Hills and elsewhere through the Canadian Rockies. *Dryas* growth commences in early May, 1-2 weeks after snowmelt. Most leaf expansion occurs through May, and new leaves begin elongating in June-July. The flowering peak is late June. Leaves overwinter in all stages of development and normally seem to last 2½ seasons.

12. Leaves are smallest and mat expansion slowest on windswept gravelly ridges. Largest leaves are found in warm and shelterd microsites. Elevation and substrate seem to have very little effect on *Dryas'* morphology.

13. Adaptations of *D. octopetala* for its typically xeric habitat include early-season peak growth, evergreen condition,

prostrate habit, vegetative mode of reproduction, retention of dead leaves on stem, densely hairy leaf underside and waxy secretion on upper surface. The ability of *Dryas* mats to absorb heat may be critical in May when ambient temperatures can be rather low; but the possible inability to maintain a lower temperature than adjacent microsites (as seen in arctic *D. integrifolia*) may be deleterious, especially during relatively hot, windy weather in August.

14. *Dryas octopetala* is a climax dominant in upland tundra in the Canadian Rockies and Arctic. Although it has the potential to thrive in mesic tundra, it is competitively excluded by heaths. At the southern end of its range both in Europe and North America, *D. octopetala* is a seral species, reportedly succeeded by graminoid communities.

15. In many communities where it provides the chief plant cover, *D. octopetala* seems critical to the success of virtually all non-saxicolous lichens and bryophytes, and of some vascular plant species. The senescing centres of *Dryas* mats provide stable microsites that are colonized first by mosses and crustose lichens, then vasculars and fruticose lichens. Competitive exclusion of early colonizers by later ones rarely occurs. Colonization is the longest phase of a simple cycle. The mats ultimately break up and the colonizer micro-communities are eroded away. The *Dryas* clones rejuvenate, and as they grow are colonized anew.

16. *D. octopetala* is much more important in a host role

than its chief mat analogues. *Salix arctica* mats are too diffuse to significantly alter the microhabitat, therefore harbor many fewer colonizers. *Empetrum nigrum* mats are too dense for many colonizers, and furthermore have a relatively depauperate invertebrate fauna. *Silene acaulis* cushions provide a favorable substrate but are relatively small and in the Bald Hills only locally abundant.

17. Where *Dryas* mat cover is at least 15%, mites especially oribatids number ca. 12,000-20,000/m^2 through the year. Collembolan numbers are much lower and much less uniform. Spiders and insects are active in June-August. *Dryas* tundra has lower beetle activity and very few bugs compared to Herb Meadow and Heath Tundra communities. Most other groups, including flies, Hymenoptera, Collembola, spiders and mites, appear as abundant in *Dryas*-dominated as in more mesic communities.

18. Arthropod activity is highest in the most mesic microsites of *D. octopetala*/lichen communities, and lowest on bare gravel patches. In *Dryas* matfields, the mats are centers of arthropod activity, though a few species of arthropods seem to shun the mats. The mats support much more uniform numbers of arthropods through the season than do hollows or gravel patches.

19. A red spider mite (*Eotetranychus* sp.) and mealybug (*Chorizococcus* sp.) are the only important *Dryas* herbivores in the Bald Hills. There is a low incidence of noctuid

larvae eating floral parts. Leaf-miner activity is extremely low. White-tailed ptarmigan may utilize *Dryas* leaves in spring and fall. Many insects particularly flies visit *Dryas* blossoms, and some species may depend on the nectar or pollen as their chief energy source. Peak insect activity in *Dryas*-dominated vegetation does not, however, coincide with the peak flowering period.

20. The relationship between *Dryas octopetala* and associated biota may be termed commensal. *Dryas* is neither benefited nor harmed, but species richness, population numbers, and possibly stability are much enhanced, in the lichen and arthropod groups in particular. As a host *Dryas* is near-perfect: abundant, stable, long-lived, tolerant. In upland alpine habitats it is an important source of food (mainly litter), warmth (in the flowers and mats), shelter and stability (*vs* surface and wind movement). The incidence of disease and phytophagy is remarkably low, and suggests allelopathic or other evolutionary mechanisms that have ensured its continued dominant role.

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APPENDIX 1. Flora of the Bald Hills.

LICHENS

LECANORALES

COLLEMATACEAE

Collema polycarpon Hoffm.
C. tenax (Sw.) Ach.

PLACYNTHIACEAE

Psoroma hypnorum (Vahl) S. Gray

PANNARIACEAE

Pannaria pezizoides (G. Web.) Trev.

PELTIGERACEAE

Peltigera aphthosa (L.) Willd.
P. canina (L.) Willd.
P. horizontalis or *polydactyla*
P. leucophlebia (Nyl.) Gyeln.
P. malacea (Ach.) Funck
P. rufescens (Weis.) Humb.
P. scabrosa Th. Fr.
P. spuria (Ach.) DC.
P. venosa (L.) Baumg.

Solorina crocea (L.) Ach.

NEPHROMATACEAE

Nephroma arcticum (L.) Torss.
N. expallidum (Nyl.) Nyl.

STICTACEAE

Lobaria linita (Ach.) Rabenh.

LECIDEACEAE

Arthrorhaphis citrinella (Ach.) Poelt
A. citrinella var. *alpina*

Bacidia alpina

Lecidea armeniaca (DC.) Fr.
L. atrobrunnea (Ram.) Schaer.
L. crustulata (Ach.) Spreng.
L. dicksonii (Gmel.) Ach.
L. glomerulosa (DC.) Steud.
L. granulosa (Ehrh.) Ach.
L. marginata Schaer.
L. rubiformis (Wahlenb. ex Ach.) Wahlenb.
L. sp.

Lecidella stigmatea (Ach.) Hert. & Leuck.

Rhizocarpon disporum (Naeg.) Müll. Arg.
R. geographicum (L.) DC.
R. macrosporum Räs.
R. sphaerosporum

STEREOCAULACEAE

Stereocaulon alpinum Laur.
S. condensatum Hoffm.
S. subalbicans Lamb

CLADONIACEAE

Cladina mitis (Sandst.) Hale & W. Culb.
C. rangiferina Wigg.

Cladonia cariosa (Ach.) Spreng.
C. cenotea (Ach.) Schaer.
C. chlorophaea (Flörke ex Somm.) Spreng.
C. coccifera (L.) Willd.
C. cornuta (L.) Hoffm.
C. decorticata (Flörke) Spreng.
C. deformis (L.) Hoffm.
C. ecmocyna (Ach.) Nyl.
C. furcata (Huds.) Schrad.
C. gonecha (Ach.) Asah.
C. macrophyllodes Nyl.
C. phyllophora Hoffm.
C. pleurota (Flörke) Schaer.
C. pocillum (Ach.) O. Rich.
C. pyxidata (L.) Hoffm.
C. subcervicornis (Vain.) Kernst.
C. uncialis (L.) Wigg.
C. cf. *verticillata* (Hoffm.) Schaer.

UMBILICARIACEAE

Omphalodiscus virginis (Schaer.) Schol.

Umbilicaria cylindrica (L.) Del.
U. hyperborea (Ach.) Ach.
U. proboscidea (L.) Schrad.
U. vellea (L.) Ach. (Scotter 10146, UAC)

PERTUSARIACEAE

Pertusaria cf. *bryophaga* Erichs.
P. coriacea (Th. Fr.) Th. Fr.
P. dactylina (Ach.) Nyl.
P. octomela (Norm.) Erichs.
P. cf. *panyrga* (Ach.) Mass.

ACAROSPORACEAE

Acarospora chlorophana (Wahlenb. ex Ach.) Mass.
A. sp.

LECANORACEAE

Haematomma lapponicum Räs.

Icmadophila ericetorum (L.) Zahlbr.

Lecanora alpina Somm.
L. badia (Hoffm.) Ach.
L. castanea (Hepp) Th. Fr.
L. chrysoleuca (Sm.) Ach.
L. frustulosa (Dicks.) Ach.
L. melanophthalma (Ram.) Ram.
L. polytropa (Ehrh.) Rabenh.
L. rupicola (L.) Zahlbr.
L. varia (Ehrh.) Ach.
L. verrucosa Ach.
L. sp.

Ochrolechia frigida (Sw.) Lynge f. *frigida*
O. geminipara (Th. Fr.) Vain.
O. upsaliensis (L.) Mass.

CANDELARIACEAE

Candelariella aurella (Hoffm.) Zahlbr. (Scotter 10140, UAC)
C. hudsonica Hak.
C. vitellina (Ehrh.) Müll. Arg.
C. sp.

PARMELIACEAE

Cetraria commixta (Nyl.) Th. Fr.
C. cucullata (Bell.) Ach.
C. ericetorum Opiz
C. hepatizon (Ach.) Vain.
C. islandica (L.) Ach.
C. nivalis (L.) Ach.
C. pinastri (Scop.) S. Gray
C. tilesii Ach.

Hypogymnia austerodes (Nyl.) Räs.
H. intestiniformis (Vill.) Räs.
H. physodes (L.) W. Wats.

Parmelia cf. *disjuncta* Erichs.
P. saxatilis (L.) Ach.
P. stygia (L.) Ach.
P. taractica Kremp.

Parmeliopsis ambigua (Wulf.) Nyl.
P. hyperopta (Ach.) Arn.

USNEACEAE

Alectoria chalybeiformis (L.) S. Gray
A. nigricans (Ach.) Nyl.
A. ochroleuca (Hoffm.) Mass.
A. pubescens (L.) R. H. Howe
A. vexillifera (Nyl.) Stizenb.

Cornicularia aculeata (Schreb.) Ach.
C. normoerica (Gunn.) Du Rietz

Dactylina arctica [PD+] (Hook.) Nyl.
D. ramulosa (Hook.) Tuck.

Letharia vulpina (L.) Hue

Thamnolia subuliformis (Ehrh.) W. Culb.

BUELLIACEAE

Buellia disciformis (Fr.) Mudd
B. papillata (Somm.) Tuck.

Rinodina nimbosa (Fr.) Th. Fr.
R. mniaraea (Ach.) Körb.
R. pyrina (Ach.) Arn.
R. roscida (Somm.) Arn.
R. turfacea (Wahlenb.) Körb.

PHYSCIACEAE

Physcia dubia (Hoffm.) Lett.
P. endococcinea (Körb.) Th. Fr.

Physconia muscigena (Ach.) Poelt

TELOSCHISTACEAE

Caloplaca jungermanniae (Vahl) Th. Fr.
C. sinapisperma (Lam.) Mah. & Gill.
C. stillicidiorum (Vahl) Lynge
C. tetraspora (Nyl.) Oliv.

Xanthoria elegans (Link) Th. Fr.
X. sorediata (Vain.) Poelt

SPHAERIALES

VERRUCARIACEAE

Dermatocarpon fluviatile (G. Web.) Th. Fr.
D. miniatum (L.) Mann

FUNGI IMPERFECTI

Lepraria membranacea (Dicks.) Vain.
L. neglecta (Nyl.) Lett.

BRYOPHYTES

HEPATICAE

JUNGERMANNIALES

LOPHOZIACEAE

Anastrophyllum (Sphenolobus) minutum Schust.

Barbilophozia hatcheri (Evans) Loeske
B. lycopodioides (Wallr.) Loeske

Chandonanthus (Temnoma) setiformis (Ehrh.) Lindb.

Leiocolea muelleri (Nees) Joerg.

Lophozia spp.

Orthocaulis cf. *atlantica* (Kaal.) Schiffn.
O. binsteadii (Kaal.) Buch

Tritomaria exsectiformis (Breidl.) Schiffn.
T. quinquedentata (Huds.) Buch
T. quinquedentata f. *gracilis* (Jens.) Schust.
T. sp.

JUNGERMANNIACEAE

Jungermannia (Solenostoma) cf. *schiffneri* (Loitl.) Evans

MARSUPELLACEAE

Gymnomitrium concinnatum (Lightf.) Corda
G. corallioides Nees

SCAPANIACEAE

Scapania irrigua (Nees) Dum.

PLAGIOCHILACEAE

Plagiochila asplenioides (L.) Dum.

HYGROBIELLACEAE

Anthelia juratzkana (Limpr.) Trav.

CEPHALOZIELLACEAE

Cephaloziella byssacea (Roth) Warnst.
C. rubella (Nees) Warnst.
C. sp.

CEPHALOZIACEAE

Cephalozia connivens (Dicks.) Lindb.
C. media Lindb.
C. sp.

PTILIDIACEAE

Ptilidium ciliare (L.) Hampe

BLEPHAROSTOMACEAE

Blepharostoma trichophyllum (L.) Dum.

MARCHANTIALES

GRIMALDIACEAE

Asterella sp.

SPHAGNA

SPHAGNALES

SPHAGNACEAE

Sphagnum angustifolium (Russ.) C. Jens.
S. compactum DC.
S. riparium Angstr.
S. russowii Warnst.
S. squarrosum Crome
S. warnstorfii Russ.

MUSCI

DICRANALES

DITRICHACEAE

Ceratodon purpureus (Hedw.) Brid.

Distichium capillaceum (Hedw.) B.S.G.

Ditrichum flexicaule (Schwaegr.) Hampe

Saelania glaucescens (Hedw.) Bomanss. & Broth.

DICRANACEAE

Amphidium lapponicum (Hedw.) Schimp.

Cynodontium schisti (Wahlenb.) Lindb.
C. strumiferum (Hedw.) Lindb.

Dichodontium pellucidum (Hedw.) Schimp.

Dicranoweisia crispula (Hedw.) Lindb. ex Milde

Dicranum acutifolium (Lindb. & H. Arnell) C. Jens. ex Weinm.
D. fuscescens Turn.
D. scoparium Hedw.
D. spadiceum Zett.

Kiaeria starkei (Hedw.) I. Hag.

Paraleucobryum enerve (Thed. ex C. J. Hartm.) Loeske

POTTIALES

ENCALYPTACEAE

Encalypta rhaptocarpa Schwaegr.
E. vulgaris Hedw.
E. sp.

POTTIACEAE

Bryoerythrophyllum recurvirostrum (Hedw.) Chen

Desmatodon latifolius (Hedw.) Brid.

Tortella fragilis (Hook. ex Drumm.) Limpr.
T. tortuosa (Hedw.) Limpr.

Tortula mucronifolia Schwaegr.
T. norvegica (Web.) Wahlenb. ex Lindb.
T. ruralis (Hedw.) Gaertn., Mayer & Scherb.

GRIMMIALES

GRIMMIACEAE

Grimmia alpicola Hedw.
G. apocarpa Hedw.
G. apocarpa var. *pulvinata* (De Not.) Lindb.
G. donniana Sm.
G. tenerrima Ren. & Card. (*G. alpestris*)
G. torquata Hornsch. ex Grev.
G. sp.

Rhacomitrium canescens (Hedw.) Brid.
R. heterostichum (Hedw.) Brid.
R. h. var. *sudeticum* (Funck) Dix. ex Bauer
R. lanuginosum (Hedw.) Brid.
R. sp.

FUNARIALES

SPLACHNACEAE

Tayloria lingulata (Dicks.) Lindb.

EUBRYALES

BRYACEAE

Bryum argenteum Hedw.
B. caespiticium Hedw.
B. pseudotriquetrum (Hedw.) Gaertn., Meyer & Scherb.
B. spp.

Pohlia cruda (Hedw.) Lindb.
P. nutans (Hedw.) Lindb.
P. wahlenbergii (Web. & Mohr) Andr.

MNIACEAE

Mnium blyttii B.S.G.
M. orthorrhynchum Brid.

Rhizomnium pseudopunctatum (Bruch & Schimp.) Koponen

AULACOMNIACEAE

Aulacomnium palustre (Hedw.) Schwaegr.

MEESIACEAE

Meesia longiseta Hedw.
M. uliginosa Hedw.

BARTRAMIACEAE

Bartramia ithyphylla Brid.

Conostomum tetragonum (Hedw.) Lindb.

Philonotis fontana (Hedw.) Brid.

TIMMIACEAE

Timmia sp.

ISOBRYALES

ORTHOTRICHACEAE

Orthotrichum laevigatum f. *macounii* (Aust.) Lawt. & Vitt
O. rupestre Schleich. ex Schwaegr.
O. speciosum Nees ex Sturm
O. sp.

HYPNOBRYALES

THELIACEAE

Myurella julacea (Schwaegr.) B.S.G.

LESKEACEAE

Lescuraea radicosa (Mitt.) Moenk.

THUIDIACEAE

Thuidium abietinum (Hedw.) B.S.G. *(Abietinella abietina)*
T. recognitum (Hedw.) Lindb.

AMBLYSTEGIACEAE

Amblystegium serpens (Hedw.) B.S.G.

Calliergon sarmentosum (Wahlenb.) Kindb.

Campylium stellatum (Hedw.) C. Jens.

Drepanocladus revolvens (Sw.) Warnst.
D. uncinatus (Hedw.) Warnst.
D. vernicosus (Lindb. ex C. Hartm.) Warnst.

BRACHYTHECIACEAE

Brachythecium salebrosum (Web. & Mohr) B.S.G.
B. turgidum (Hartm.) Kindb.
B. cf. *velutinum* (Hedw.) B.S.G.
B. sp.

Cirriphyllum cirrosum (Schwaegr. ex Schultes) Grout

Eurhynchium pulchellum (Hedw.) Jenn.

Tomenthypnum nitens (Hedw.) Loeske

PLAGIOTHECIACEAE

Plagiothecium denticulatum (Hedw.) B.S.G.

HYPNACEAE

Hypnum procerrimum Mol.
H. revolutum (Mitt.) Lindb.

RHYTIDIACEAE

Rhytidium rugosum (Hedw.) Kindb.

HYLOCOMIACEAE

Hylocomium splendens (Hedw.) B.S.G.

POLYTRICHALES

POLYTRICHACEAE

Oligotrichum parallelum (Mitt.) Kindb.

Pogonatum urnigerum (Hedw.) P. Beauv.

Polytrichastrum alpinum (Hedw.) G.L. Smith
(Pogonatum alpinum)
P. a. var. *septentrionale* (Brid.) G.L. Smith
(Polytrichum norvegicum)
P. lyallii (Mitt.) G.L. Smith
(Polytrichadelphus lyallii)

Polytrichum commune Hedw.
P. juniperinum Hedw.
P. piliferum Hedw.

VASCULAR PLANTS

LYCOPODIACEAE

Lycopodium alpinum L.
L. annotinum L.
L. clavatum L.
L. selago L.

SELAGINELLACEAE

Selaginella densa Rydb.

EQUISETACEAE

Equisetum variegatum Schleich.

OPHIOGLOSSACEAE

Botrychium lunaria (L.) Swartz

POLYPODIACEAE

Cystopteris fragilis (L.) Bernh.

Gymnocarpium dryopteris (L.) Newm.

Polystichum lonchitis (L.) Roth.

CUPRESSACEAE

Juniperus communis L.

PINACEAE

Abies lasiocarpa (Hook.) Nutt.

Picea engelmannii Parry ex Engelm.

Pinus contorta Dougl. ex Loud. var. *latifolia* Engelm.

JUNCACEAE

Juncus drummondii E. Meyer
J. mertensianus Bong.

Luzula arcuata (Wahlenb.) Sw.
L. parviflora (Ehrh.) Desv.
L. spicata (L.) DC.
L. wahlenbergii Rupr.

CYPERACEAE

Carex albonigra Mack.
C. atrata L.
C. bipartita All.
C. brevipes Boott
C. brunnescens (Pers.) Poir.
C. eleusinoides Turcz. ex C. A. Mey. *(C. eurystachya)*
C. glacialis Mack.
C. haydeniana Olney
C. incurviformis Mack.
C. misandra R. Br.
C. nardina Fries
C. nigricans C. A. Mey.
C. paupercula Michx.
C. paysonis Clokey
C. phaeocephala Piper
C. pyrenaica Wahlenb.
C. rupestris Allioni var. *drummondiana* (Dewey) Bailey
C. saxatilis L. *(C. physocarpa)*
C. spectabilis Dewey (incl. *C. tolmiei*)

Eriophorum polystachion L. *(E. angustifolium)*
E. scheuchzeri Hoppe
E. viridicarinatum (Engelm.) Fern.

Kobresia bellardii (Allioni) Degland. *(K. myosuroides)*

GRAMINEAE

Agropyron latiglume Rydb.

Agrostis variabilis Rydb.

Calamagrostis inexpansa Gray
C. purpurascens R. Br.

Danthonia intermedia Vasey

Deschampsia atropurpurea (Wahlenb.) Scheele
D. cespitosa (L.) Beauv.

Elymus innovatus Beal

Festuca brachyphylla Schultes

Hierochloe alpina (Sw.) R. & S.

Phleum alpinum L.

Poa alpina L.
P. cusickii Vasey (incl. *P. epilis*)
P. grayana Vasey (*P. arctica, P. longipila*)
P. interior Rydb.
P. lettermanii Vasey
P. pattersonii Vasey
P. rupicola Nash
P. scabrella (Thurb.) Benth. ex Vasey (*P. canbyi*)
P. sp.

Trisetum spicatum (L.) Richter

LILIACEAE

Veratrum viride Ait. var. *eschscholtzii* (R. & S.) Breitung

SALICACEAE

Populus tremuloides Michx.

Salix arctica Pall.
S. barrattiana Hook.
S. glauca L. var. *villosa* (Hook.) Anderss.
S. nivalis Hook.
S. vestita Pursh

BETULACEAE

Betula glandulosa Michx.

POLYGONACEAE

Eriogonum androsaceum Benth.

Oxyria digyna (L.) Hill

Polygonum viviparum L.

PORTULACACEAE

Claytonia lanceolata Pursh

CARYOPHYLLACEAE

Arenaria obtusiloba (Rydb.) Fern.
A. rossii R. Br.
A. rubella (Wahlenb.) J. E. Smith

Cerastium beeringianum Cham. & Schlecht.

Lychnis apetala L.

Sagina saginoides (L.) Britt.

Silene acaulis L.

Stellaria calycantha (Ledeb.) Bong.
S. longipes Goldie (incl. *S. monantha*)

RANUNCULACEAE

Anemone drummondii Wats.
A. occidentalis Wats.
A. parviflora Michx.

Aquilegia flavescens Wats.

Caltha leptosepala DC.

Ranunculus eschscholtzii Schlecht.
R. gelidus Kar. & Kir.
R. nivalis L.
R. pygmaeus Wahlenb.

Trollius laxus Salisb. (*T. albiflorus*)

PAPAVERACEAE

Papaver kluanensis D. Löve

CRUCIFERAE

Arabis drummondii Gray
A. lyallii Wats.
A. lyrata L.

Cardamine bellidifolia L.
C. oligosperma Nutt.

Draba aurea Vahl.
D. crassifolia R. Grah.
D. incerta Pays.
D. lanceolata Royle
D. lonchocarpa Rydb. (incl. *D. nivalis*)
D. paysonii Macbr.
D. praealta Greene

Erysimum pallasii (Pursh) Fern.

CRASSULACEAE

Sedum lanceolatum Torr.

SAXIFRAGACEAE

Leptarrhena pyrolifolia (D. Don) R. Br. ex Ser.

Parnassia fimbriata Konig.

Saxifraga adscendens L.
S. bronchialis L.
S. caespitosa L.
S. cernua L.
S. debilis Engelm. ex Gray (*S. rivularis*)
S. lyallii Engl.
S. occidentalis Wats.
S. oppositifolia L.
S. punctata L. (*S. aestivalis*)

ROSACEAE

Dryas octopetala L. ssp. *hookeriana* (Juz.) Hultén

Fragaria virginiana Duchesne

Luetkea pectinata (Pursh) Kuntze

Potentilla diversifolia Lehm.
P. hyparctica Malte
P. nivea L.
P. uniflora Ledeb.
P. villosa Pall. ex Pursh

Rosa acicularis Lindl.

Rubus idaeus L.

Sibbaldia procumbens L.

LEGUMINOSAE

Astragalus aboriginum Richards.
A. alpinus L.
A. vexilliflexus Sheld.

Oxytropis campestris (L.) DC.
O. podocarpa A. Gray

EMPETRACEAE

Empetrum nigrum L.

ELAEAGNACEAE

Shepherdia canadensis (L.) Nutt.

ONAGRACEAE

Epilobium alpinum L.
E. a. var. *clavatum* (Trel.) C. L. Hitchc. (*E. clavatum*)
E. a. var. *lactiflorum* (Hausskn.) C. L. Hitchc. (*E. lactiflorum*)
E. a. var. *nutans* (Hornem.) Hook. (*E. hornemannii*)
E. angustifolium L.
E. latifolium L.

ERICACEAE

Arctostaphylos uva-ursi (L.) Spreng.

Cassiope mertensiana (Bong.) D. Don
C. tetragona (L.) D. Don

Kalmia polifolia Wang. var. *microphylla* (Hook.) Rehd.

Ledum groenlandicum Oeder

Phyllodoce empetriformis (Sw.) D. Don
P. glanduliflora (Hook.) Coville

Vaccinium caespitosum Michx.
V. scoparium Leiberg
V. vitis-idaea L.

PRIMULACEAE

Androsace septentrionalis L.

GENTIANACEAE

Gentiana glauca Pallas
G. glauca (yellow-flowered form)
G. propinqua Richards. (*Gentianella propinqua*)
G. prostrata Haenke (*Gentiana fremontii*)

BORAGINACEAE

Myosotis sylvatica Hoffm. var. *alpestris* (F. W. Schmidt) Koch

SCROPHULARIACEAE

Castilleja occidentalis Torr.
C. rhexifolia Rydb.

Pedicularis arctica R. Br.
P. bracteosa Benth.
P. groenlandica Retz.

Penstemon ellipticus Coult. & Fish.

Veronica wormskjoldii Roem. & Schult. *(V. alpina)*

VALERIANACEAE

Valeriana sitchensis Bong.

CAMPANULACEAE

Campanula lasiocarpa Cham.

COMPOSITAE

Achillea millefolium L.

Agoseris aurantiaca (Hook.) Greene

Antennaria alpina (L.) Gaertn.
A. lanata (Hook.) Greene
A. umbrinella Rydb.

Arnica alpina (L.) Olin
A. cordifolia Hook.
A. diversifolia Greene
A. latifolia Bong.
A. latifolia var. *gracilis* (Rydb.) Cronq.
A. louiseana Farr
A. mollis Hook.
A. rydbergii Greene

Artemisia michauxiana Bess.
A. norvegica Fries

Aster sibiricus L.

Crepis nana Rich.

Erigeron acris L. var. *debilis* Gray
E. aureus Greene
E. compositus Pursh
E. humilis Graham
E. pallens Cronq.
E. peregrinus (Pursh) Greene

Hieracium gracile Hook.

Petasites frigidus (L.) Fries *(P. palmatus)*

Saussurea densa (Hook.) Rydb.

Senecio fremontii T. & G.
S. pauciflorus Pursh
S. triangularis Hook.

Solidago multiradiata Ait.

Taraxacum lyratum (Ledeb.) DC.
T. sp.

APPENDIX 2. Arthropods collected in the Bald Hills.

CRUSTACEA

CALANOIDA

DIAPTOMIDAE

Diaptomus shoshone S. A. Forbes

DIPLOPODA

CHORDEUMIDA

CONOTYLIDAE

Conotyla albertana Chamberlin
C. atrolineata (Bollman)

CHILOPODA

LITHOBIOMORPHA

LITHOBIIDAE

Lophobius cf. *helenae* Chamberlin
L. sp.

Nadabius cf. *ameles* Chamberlin

?*Oabius* sp.

INSECTA

COLLEMBOLA

PODURIDAE

Hypogastrura cf. *manubrialis* (Tullberg)
H. socialis (Uzel)

Morulina sp. nr. *gigantea* (Tullberg)
M. ?n. sp.

Onychiurus subtenuis (Folsom)
O. sp.

ENTOMOBRYIDAE

Entomobrya cf. *comparata* Folsom
E. nivalis (L.)
E. n. sp.
E. sp.

Folsomia quadrioculata (Tullberg)

Isotoma grandiceps Reuter
I. violacea (Tullberg)
I. viridis (Bourlet)
I. sp.

Isotomurus palustris (Müller)

Proisotoma sp.

Tomocerus flavescens (Tullberg)

SMINTHURIDAE

Bourletiella hortensis (Fitch)

Deuterosminthurus repandus Agren

EPHEMEROPTERA

HEPTAGENIIDAE

Stenonema cf. *exiguum* Traver

ORTHOPTERA

ACRIDIDAE

Melanoplus borealis (Fieber)

GRYLLOBLATTIDAE

Grylloblatta campodeiformis Walker

PLECOPTERA

TAENIOPTERYGIDAE

undet. gen.

PERLIDAE

Isoperla fusca Needham & Claassen

Megarcys watertoni Ricker

Paraperla wilsoni Ricker

Zapoda columbiana (Claassen)

THYSANOPTERA

THRIPIDAE

Anaphothrips secticornis (Trybom)

Aptinothrips rufus (Gmelin)
A. stylifer Trybom

Frankliniella cf. *achaeta* Hood
F. occidentalis (Pergande)

Oxythrips sp.

Taeniothrips orionis Treherne

HEMIPTERA

ANTHOCORIDAE

Orius tristicolor (White)

MIRIDAE

Deraeocoris sp.

Lygus sp.

Plagiognathus sp.

Trigonotylus sp.

undet. nymphs

LYGAEIDAE

Geocoris bullatus (Say)
G. sp.

Nysius thymi (Wolff)

HOMOPTERA

CICADELLIDAE

Empoasca sp.

Latalus sp.

Scleroracus sp.

PSYLLIDAE

Psylla americana Crawford
P. striata Patch

Trioza sp.

undet. nymphs

APHIDIDAE

Acyrthosiphon sp.

Amphorophora n. sp.
A. sp.

Cinara spp.

Dactynotus cf. *nigrotuberculatus* Olive

Kakimia alpina (G. & P.)
K. n. sp.

Macrosiphum sp.

Mindarus abietinus (Koch)

Myzodium modestum Hottes
M. sp. nr. *modestum* (Hottes)

Pterocomma bicolor (Oestlund) ssp. *groenlandicus* HRL

ERIOSOMATIDAE

Pemphigus sp.

PSEUDOCOCCIDAE

Chorizococcus sp. nr. *altoarcticus* (Richards)

Pseudococcus sp.

nymphs

COCCOIDEA

undet. spp. (3+)

NEUROPTERA

CONIOPTERYGIDAE

Conwentzia sp.

Wesmaelius longifrons (Walker)

undet. genus

HEMEROBIIDAE

Helicoconis lutea Wall.

Hemerobius sp.

COLEOPTERA

CARABIDAE

Amara discors Kby.

Bembidion complanulum Man.
B. grapei Gyllenhal
B. sp. (*incertum* grp.)
B. sp.

Carabus taedatus agassii LeC.

Dyschirius sp.

Nebria intermedia Van Dyke

Notiophilus aquaticus (L.)
N. directus Csy.
N. intermedius Lindroth
N. sp.

Pterostichus haematopus Dej.

DYTISCIDAE

Agabus inscriptus (Crotch)

Hydroporus morio Sharp
H. occidentalis Sharp

LEIODIDAE

Hydnobius cf. *lobatus* Hatch
H. cf. *matthewsii* Crotch

Leiodes sp.

STAPHYLINIDAE

Acidota quadrata Zett.

Acrolocha prob. n. sp.

Aleochara bimaculata Gyll.

Anthobium sp.

Arpedium brunnescens J. Sahlb.
A. tenue (LeC.)

Atheta sp.

Lordithon rubescens Hatch
L. sp.

Mycetoporus prob. n. sp.
M. sp.

Phlaeopterus prob. n. sp.

Quedius densiventris (Csy.)
Q. sp.

Stenus sp.

Tachinus contortus Hatch
T. elongatus Gyll.

CANTHARIDAE

Malthodes sp. nr. *idahoensis* Fend.

Podabrus extremus LeC.
P. tetragonoderus Fall

ELATERIDAE

Hypolithus bicolor Esch.

Negastrius tumescens (LeC.)

BYRRHIDAE

Byrrhus fasciatus Forster (*B. stolidus* Csy.)
B. kirbyi LeC. (*B. wickhami* Csy.)

Simplocaria remota Brown
S. tessellata LeC.

NITIDULIDAE

Thalycra concolor (LeC.)

LATHRIDIIDAE

Lathridius minutus L.

COCCINELLIDAE

Coccinella novemnotata Hbst.

Hippodamia oregonensis Crotch.

Hyperaspis n. sp.

SALPINGIDAE

Sphaeriestes alternatus (LeC.)

SCARABAEIDAE

Aphodius congregatus Mann.
A. sp.

CERAMBYCIDAE

Callidium sp.

Cortodera longicornis (Kirby)

Pachyta lamed L.

CHRYSOMELIDAE

Chrysomela sp.

Gonioctena nivosa alberta Brown
G. nivosa arctica Mann.
G. spp.

Hydrothassa borella Schaeff.

TRICHOPTERA

LIMNEPHILIDAE

Asynarchus lapponicus Zett.

Lenarchus fautini Denn.

Limnephilus hyalinus Hagen

LEPIDOPTERA

PIERIDAE

Colias alexandra christina Edwards
C. nastes streckeri Gr.
C. pelidne minisni Bean

SATYRIDAE

Oeneis polixenes brucei (Edwards)

NYMPHALIDAE

Boloria eunomia dawsoni (Barnes & McDunnough)
B. titania boisduvalii (Dup.)
B. titania grandis (Barnes & McDunnough)

Euphydryas editha beani (Skin.)

Nymphalis milberti milberti (Godart)

Speyeria mormonia bischoffii (Edwards)

LYCAENIDAE

Lycaeides argyrognomon scudderii (Edwards)

HESPERIIDAE

Pyrgus centaureae (Rambur)

ARCTIIDAE

Pararctia lapponica yarrowii (Stretch)

NOCTUIDAE

Anarta cordigera (Thun.)
A. melanopa (Thun.)

Autographa californica Spey.

?*Copablepharon viridisparsa* Dod.

?*Faronta diffusa* Wlk.

?*Spaelotis clandestina* Harr.

Syngrapha orophila Hamp.

?Zosteropoda hirtipes Grt.

GEOMETRIDAE

?Xanthorhöe sp.

undet. genera

PYRALIDAE

Loxostege sp. prob. *commixtalis* Wlk.

COLEOPHORIDAE

Coleophora sp.

TINEIDAE

undet. genus

NEPTICULIDAE

Nepticula spp.

DIPTERA

TRICHOCERIDAE

Trichocera columbiana Alex.
T. sp.

TIPULIDAE

Chionea albertensis Alex.
C. alexandriana Garrett

Tipula (Pterelachisus) sp. A
T. (P.) sp. B
T. (P.) sp.
T. (Vestiplex) arctica Curtis
T. (V.) leucophaea Doane
T. (V.) platymera Walk.

NYMPHOMYIIDAE

Oreadomyia albertae Kevan

CULICIDAE

Aedes cataphylla Dyar
A. impiger (Wlk.)
A. pullatus (Coq.)

CERATOPOGONIDAE

Ceratopogon (Ceratopogon) n. sp.

Culicoides yukonensis Hoffman

Dasyhelea sp. 1
D. sp. 2

Forcipomyia sp.

CHIRONOMIDAE

Chaetocladius sp.

Cricotopus sp.

Gymnometriocnemus sp.

Micropsectra sp.

Smittia cf. *paranudipennis* Brundin
S. n. sp.

SIMULIIDAE

Prosimulium fulvum (Coq.)
P. cf. *travisi* Stone

Simulium arcticum Malloch
S. hunteri Malloch
S. tuberosum Lund.

Twinnia nova (Dyar & Shannon)

BIBIONIDAE

Bibio sp. nr. *nigritus* Curran & *striatipes* Walker
B. sp.

MYCETOPHILIDAE

Allodia sp.

Boletina longicornis Joh.
B. sp. A
B. sp. B
B. sp. 6
B. sp. 19
B. sp. 20

Cordyla sp.

Docosia sp.

Exechia sp.

Mycetophila fungorum (Deg.)
M. ichneumonea Say

Mycomya sp. A
M. sp. B
M. sp.

Rymosia cristata (Staeg)
R. tarnanii Dzied

new genus

SCIARIDAE

Bradysia spp. (4+)

CECIDOMYIIDAE

CECIDOMYINAE

LESTREMIINAE

undet. spp.

TABANIDAE

Hybomitra lanifera (McDunnough)
H. osburni (Hine)

RHAGIONIDAE

Ptiolina alberta Leonard

THEREVIDAE

Thereva cf. *brunnea* Cole

EMPIDIDAE

Anthepiscopus n. sp.

Charadrodromia n. sp.

Iteaphila sp.

Hilara sp.

Platypalpus prorsus Mel.

Rhamphomyia (Megacyttarus) sp.
R. (Pararhamphomyia) sp. 1
R. (P.) sp. 2

Tachypeza n. sp.

undet. genus (Tachydromiinae)

PHORIDAE

Diplonevra n. sp.

Megaselia (Aphiochaeta) spp.
M. (M.) sp.

Triphleba palposa (Zett.)

PLATYPEZIDAE

Microsania sp.

SYRPHIDAE

Arctophila flagrans O.S.

Chrysotoxum sp.

Eristalis tenax (L.)

Helophilus hybridus Loew
H. latifrons Loew

Melanostoma sp.

Metasyrphus aberrantis (Cn.)
M. lapponicus (Zett.)

Phalacrodira sp.

Platycheirus albimanus (Fab.)
P. sp.

Scaeva pyrastri (L.)

Sericomyia militaris Walk.

Sphaerophoria sp.

Syrphus torvus O.S.
S. sp.

DRYOMYZIDAE

Dryomyza setosa (Bigot)

PIOPHILIDAE

Mycetaulus nigritellus Melander

SPHAEROCERIDAE

Copromyza equina Fall.

Leptocera fontinalis (Fall.)
L. sp. 1
L. sp. 2

EPHYDRIDAE

Philygria debilis Lw.

AGROMYZIDAE

Phytomyza demissa Spen.
P. sp. 1
P. sp. 2

HELEOMYZIDAE

Aecothea sp.

Heleomyza difficilis Gill

Orbellia barbata (Garrett)

ANTHOMYIIDAE

Azelia macquarti (Staeger)

Eremomyioides setosa (Stein)

Helina cinerella (van der Wulp)
H. fulvisquama (Zett.)
H. squalens (Zett.)

Hydrophoria cf. *altilega* Huckett
H. sp. nr. *verticina* (Zett.)

Hylemya platura (Meig.)
H. (Botanophila) sp.
H. (Delia) sp.
H. sp.

Lasiops albibasalis (Zett.)
L. furcatus (Stein)
L. lividiventris (Zett.)
L. spiniger (Stein)
L. subrostratus (Zett.)

Paregle cinarella (Fall.)

Pegomyia sp. (*lipsia* grp.)
P. sp.

Phaonia alticola Mall.
P. morio (Zett.)
P. protuberans (Mall.)
P. rugia (Walk.)

Quadrularia laetifica (R.-D.)

Spilogona sp. nr. *melanosoma* & *latilamina*
S. sp. A
S. sp. B

SCATOPHAGIDAE

Microprosopa diversipes Cn.

Scatophaga furcata (Say)

MUSICIDAE

Pogonomyia sp.

CALLIPHORIDAE

Acronesia anana Hall

Cynomya cadaverina R.-D.

Eucalliophora lilaea (Walk.)

Francilia fuscipalpis (Zett.)

SARCOPHAGIDAE

Agria housei Shew.

Wohlfahrtia vigil (Walk.)

TACHINIDAE

Allophorocera n. sp.

Arctophyto marginalis Cn.

Chaetovoria seriata (Ald.)

Gonia (Onychogonia) fissiforceps Toth.

Istocheta claripennis (Rnh.)

Linnaemya varia Cn.

Peleteria angulata Cn. or *posticata* Cn.
P. bryanti Cn.
P. curriei (Tnsd.)

Periscepsia cf. *helymus* (Wlk.)
P. n. sp.

undet. genus

HYMENOPTERA

TENTHREDINIDAE

Amauronematus sp. nr. *boreoalpina* (Lindqvist)
A. variator (Ruthe)
A. sp.

Pristophora borea (Knw.)
P. breadalbanensis (Cameron)
P. gelida Wong
P. n. sp.

Pteronidea sp.

Tenthredo anomocera Roh.
T. originalis (Nort.)
T. sp.

SIRICIDAE

Urocerus albicornis (F.)
U. gigas flavicornis (F.)

BRACONIDAE

Apanteles yakutatensis Ashmead
A. sp. 54
A. sp. 110
A. n. sp.

Aphidius nigripes Ashmead
A. sp.

Aspilota sp.

Colastes sp.

Dacnusa sp.

Hormius sp.

Ichneutes n. sp.

Meteorus leviventris Wesm.

Microplitis n. sp. a
M. n. sp. b

Monoctonus n. sp.

Orgilus n. sp.

Praon aguti Smith

Rogas n. sp.

ICHNEUMONIDAE

Aclastus sp.

Aculichneumon (Crypteffigies) confusus (Ashm.)

Agrothereutes abbreviator rufopectus Cush.

Alexeter spp.

Atractodes spp.

Bathythrix n. sp.

Barycnemis bellator Muller
B. sp.

Buathra laborator altonii (D.T.)

Campodorus sp.

Campoletis spp.

Campoplex sp.

Coelichneumonops cashmani Heinr.
C. occidentalis (Roman)
C. solutus (Holmg.)

Cremnodes sp.

Cryptus arcticus Schiødte

Ctenochira infans Tow. & Tow.

Cylloceria lugubris (Cress.)
C. sp.

Delomerista texana (Cress.)

Diadegma sp.

Endasys sp.

Eusterinx sp.

Exochus evetriae Roh.

Gelis spp.

Glypta sp.

Hemiteles sp.

Hybophorellus injucundus nearcticus Heinr.

Ichneumon approximans Prov.
I. sp.

Lamachus sp.

Lathrostizus sp.

Lissonata sp.

Lysibia sp.

Medophron sp.

Meloboris sp.

Mesochorus agilis Cress.
M. gelidus gelidus Dasch

Mesoleius spp.

Mesoleptus sp.

Neostroblia spp.

Neurateles sp.

Obisiphaga sp.

Olesicampe sp.

Oresbius sp.

Orthocentrus abdominalis (Prov.)
O. sp.

Phaeogenes sp.

Phygadeuon spp.

Pimpla sodalis

Plectiscidea sp.

Polyblastus (Polyblastus) strobilator (Thunb.)

Scopesis spp.

Stenomacrus spp.

Stibeutes sp.

Stilpnus sp.

Synodites sp.

undet. Gelini

MYMARIDAE

Anagrus armatus Ashmead
A. ?n. sp.

Gonatocerus sp.

TRICHOGRAMMATIDAE

Trichogramma minutum

EULOPHIDAE

Achrysocharella sp.

Chrysocharis (Chrysocharis) sp.

Cirrospilus ?n. sp.

Diglyphus begini (Ashmead)
D. websteri Crawford

Euderus (E.) cushmani (Crawford)

Prospaltella ?n. sp.

Tetrastichus sp.

ENCYRTIDAE

Copidosoma sp.

Microterys sp. nr. *physokermis* Compere
M. sp.

Ooencyrtus sp.

Pseudoencyrtus sp.

Stemmatosteres kuchari Yoshimoto

Tetracnemus ?n. sp.
T. sp.

PTEROMALIDAE

Gastrancistrus autumnalis (Walker)
G. sp.

Habrocytus sp.

Mesopolobus sp.

Pachyneuron sp.

CYNIPIDAE

Alloxysta sp.

Calofigites sp.

PROCTOTRUPIDAE

Codrus sp.

Cryptoserphus sp.

Phaenoserphus sp.

CERAPHRONIDAE

Aphanogmus sp.

Ceraphron sp.

Conostigmus sp.

Lygocerus sp.

DIAPRIIDAE

Aclista sp.

Basalys sp.

Miota sp.

Opazon sp. A.

Pantoclis sp.

Pantolyta sp.

Zygota sp. A
Z. sp. B

SCELIONIDAE

Telenomus sp.

Trimorus sp.

PLATYGASTRIDAE

Allotropa sp.

Platygaster sp.

FORMICIDAE

Camponotus herculeanus (L.)
C. noveboracensis (Fitch)

Formica fusca L.
F. sp.

Lasius sitkaensis Perg.

Leptothorax (Mycothorax) canadensis Prov.

Myrmica lobicornis fracticornis Emery

VESPIDAE

Vespula acadica (Sladen)
V. norvegicoides (Sladen)

ANDRENIDAE

Andrena ?fulvicrista Vier.

HALICTIDAE

Lasioglossum sp.

MEGACHILIDAE

Osmia sp. nr. *brevis* Cr.

APIDAE

Bombus kirbyellus Curt.
B. melanopygus Nyl.
B. mixtus Cress.
B. polaris Curt.
B. sylvicola Kby.

Psithyrus fernaldae Franklin

ARACHNIDA

PHALANGIDA

PHALANGIIDAE

Leptobunus sp.

ACARINA

PARASITIFORMES

MESOSTIGMATA

CYRTOLAELAPIDAE

Gamasellus sp.

HAEMOGAMASIDAE

Haemogamasus sp.

PHYTOSEIIDAE

Amblyseius sp.

TRACHYTIDAE

Trachytes sp.

ZERCONIDAE

Zercon sp. 1
Z. sp. 2
Z. sp. 3
Z. sp. 4

PARASITOIDEA

undet. genus

ACARIFORMES

ACARIDEI

RHIZOGLYPHIDAE

Schwiebea sp.

PROSTIGMATA

ANYSTIDAE

Anystis sp.

BDELLIDAE

Bdella longicornis
B. muscorum
B. sp.

Cyta sp.

EREYNETIDAE

Ereynetes sp.

ERYTHRAEIDAE

Abrolophus sp.

Erythraeus sp.

EUPODIDAE

Cocceupodes sp.

Eupodes sp.

NANORCHESTIDAE

Speleorchestes sp.

PACHYGNATHIDAE

Bimichaelia sp.

Pachygnathus sp.

PENTHALODIDAE

Penthalodes sp.

RHAGIDIIDAE

Rhagidia sp.

STIGMAEIDAE

Ledermuelleria sp.

Mediolata sp.

Stigmaeus sp.

TETRANYCHIDAE

Bryobia sp.

Eotetranychus sp. (*tiliarum* grp.)

TROMBIDIIDAE

Microtrombidium sp.

Podothrombium malignum Vercammen-Grandjean

TYDEIDAE

Lorryia sp.

Paralorryia sp.

Paratriophtydeus sp.

Tydeus sp.

ORIBATEI

AUTOGNETIDAE

Autogneta sp.

BRACHYCHTHONIIDAE

Eobrachychthonius sp.

CAMISIIDAE

Camisia sp. 1
C. sp. 2

Neonothrus sp.

Nothrus sp.

CERATOZETIDAE

Dentizetes sp.

Hammeria sp.

Iugoribates sp.

DAMAEIDAE

Epidamaeus sp. 1
E. sp. 2

Hungarobelba sp.

EREMAEIDAE

Eremaeus sp. 1
E. sp. 2

Eremulus sp.

LIMNOZETIDAE

Limnozetes sp.

MALACONOTHRIDAE

Trimalaconothrus sp.

MYCOBATIDAE

Mycobates sp.

NOTHRIDAE

Nothrus sp.

OPPIIDAE

Oppia sp.

ORIBATELLIDAE

Oribatella sp.

ORIBATULIDAE

Hemileius sp.

PARAKALUMNIDAE

Neoribatus sp.

TECTOCEPHEIDAE

Tectocepheus sp.

TEGORIBATIDAE

Lepidozetes sp.

TENUIALIDAE

Tenuiala sp.

THYRISOMIDAE

Oribella sp.

TRHYPOCHTHONIIDAE

Trhypochthonius sp.

ARANEIDA

AMAUROBIIDAE

Arctobius agelenoides (Emerton)

DICTYNIDAE

Argenna lorna Chamberlin & Gertsch

Dictyna sp. nr. *borealis* (Pickard-Cambridge)
D. cavernosa Jones

Lathys alberta Gertsch

GNAPHOSIDAE (DRASSIDAE)

Gnaphosa holmi Tullgren
G. microps Holm
G. muscorum (Koch)

Micaria hesperella Gertsch & Jellison

Zelotes sp. nr. *hentzi* Barrows
Z. subterraneus (Koch)

CLUBIONIDAE

Clubiona praematura Emerton
C. riparia Koch

THOMISIDAE

Philodromus alascensis Keyserling

Xysticus durus (Soerensen)
X. labradorensis Keyserling
X. luctuosus (Blackwall)

SALTICIDAE

Escambia ?n. sp.

Habronattus sp.

Icius sp.

Neon nellii Peckham & Peckham

Sitticus saxicola (Koch)
S. sp.

Stoidis sp.

Talavera minuta (Banks)

AGELENIDAE

Agelenopsis utahana Chamberlin & Ivie

HAHNIIDAE

Hahnia glacialis (Soerensen)

LYCOSIDAE

Arctosa insignita (Thorell)

Melocosa fumosa (Emerton)

Pardosa sp. nr. *anomala* Gertsch
P. n. sp. nr. *distincta* (Blackwall)
P. furcifera (Thorell)
P. fuscula (Thorell)
P. groenlandica complex
P. lapponica (Thorell)
P. sp. nr. *modica* (Blackwall)
P. moesta Banks
P. saltuaria complex
P. solitaria Levi & Levi
P. uintana Gertsch
P. ?n. sp. nr. *uintana* Gertsch
P. uncata (Thorell)
P. n. sp. 1
P. n. sp. 2

THERIDIIDAE

Theridion sp.

ARANEIDAE

Aculepeira sp. nr. *aculeata* (Emerton)

LINYPHIIDAE

Agyneta cauta (Pickard-Cambridge)

Caledonia evansi Pickard-Cambridge

Ceraticelus sp. nr. *atriceps* (Pickard-Cambridge)
C. sp. 1
C. sp. 2

Ceratinella sp.

Ceratinopsis labradorensis Emerton

Cnephalocotes obscurus (Blackwall)

Cochlembolus alpinus (Banks)
C. sacer Crosby

Collinsia sp.

Cornicularia cf. *communis* Emerton
C. directa (Pickard-Cambridge)
C. karpinskii (Pickard-Cambridge)

Erigone n. sp. nr. *zographica* Crosby & Bishop
E. n. sp.

Eularia sp.

Hilaria sp.

Islandiana falcifica (Keyserling)

Lepthyphantes arboreus (Emerton)
L. complicatus (Emerton)
L. pollicaris Zorsch

Linyphantes n. sp.

Meioneta sp.

Minyriolus castaneus (Emerton)

Oreonetides vaginatus (Thorell)

Pityohyphantes phrygianus (Koch)

Rhaebothorax n. sp. nr. *broccus* (Koch)
R. sp.

Sciastes sp.

Scylaceus obtusus (Emerton)

Sisicottus montanus (Emerton)

Sisis rotundus (Emerton)

Smodix reticulatus (Emerton)

Tiso aestivus (Koch)

Typhochraestus pygmaeus (Soerensen)
T. sp.

Walckenaera sp.

undet. genus nr. *Helophora*

undet. genera

APPENDIX 3. Vertebrate fauna of the Bald Hills.

AVES

ACCIPITRIDAE		
Accipiter striatus Vieillot	Sharp-shinned Hawk	u
Aquila chrysaetos (Linnaeus)	Golden Eagle	(B)
Buteo lagopus (Pontoppidan)	Rough-legged Hawk	m
Circus cyaneus (Linnaeus)	Marsh Hawk	m
FALCONIDAE		
Falco mexicanus Schlegal	Prairie Falcon	(B)
F. peregrinus Tunstall	Peregrine Falcon	u
F. sparverius Linnaeus	Sparrow Hawk	m
TETRAONIDAE		
Dendragapus obscurus (Say)	Blue Grouse	S
Lagopus lagopus (Linnaeus)	Willow Ptarmigan	B
L. leucurus (Richardson)	White-tailed Ptarmigan	B
CHARADRIIDAE		
Charadrius vociferus Linnaeus	Killdeer	m
Pluvialis dominica (Müller)	American Golden Plover	m
SCOLOPACIDAE		
Calidris bairdii (Coves)	Baird's Sandpiper	m
Heteroscelus incanus (Gmelin)	Wandering Tattler	m
STRIGIDAE		
Asio otus (Linnaeus)	Long-eared Owl	u
Strix nebulosa Forster	Great Gray Owl	u
TROCHILIDAE		
Selasphorus rufus (Gmelin)	Rufous Hummingbird	S
TYRANNIDAE		
Nuttallornis borealis (Swainson)	Olive-sided Flycatcher	u

Sayornis saya (Bonaparte)	Say's Phoebe	m
<u>ALAUDIDAE</u>		
Eremophila alpestris (Linnaeus)	Horned Lark	B
<u>HIRUNDINIDAE</u>		
Hirundo rustica Linnaeus	Barn Swallow	B
Petrochelidon pyrrhonota (Vieillot)	Cliff Swallow	S
<u>CORVIDAE</u>		
Corvus corax Linnaeus	Common Raven	(B)
Cyanocitta stelleri (Gmelin)	Steller's Jay	u
Nucifraga columbiana (Wilson)	Clark's Nutcracker	(B)
Perisoreus canadensis (Linnaeus)	Gray Jay	S
<u>PARIDAE</u>		
Parus atricapillus Linnaeus	Black-capped Chickadee	S
P. gambeli Ridgway	Mountain Chickadee	S
P. hudsonicus Forster	Boreal Chickadee	S
<u>SITTIDAE</u>		
Sitta canadensis Linnaeus	Red-breasted Nuthatch	S
<u>CINCLIDAE</u>		
Cinclus mexicanus Swainson	Dipper	S
<u>TROGLODYTIDAE</u>		
Troglodytes troglodytes (Linnaeus)	Winter Wren	m
<u>TURDIDAE</u>		
Catharus fuscescens (Stephens)	Veery	(B)
C. guttatus (Pallas)	Hermit Thrush	B
Ixoreus naevius (Gmelin)	Varied Thrush	S
Myadestes townsendi (Audubon)	Townsend's Solitaire	(B)
Sialia currucoides (Bechstein)	Mountain Bluebird	(B)
Turdus migratorius Linnaeus	American Robin	B
<u>SYLVIIDAE</u>		
Regulus calendula (Linnaeus)	Ruby-crowned Kinglet	S

MOTACILLIDAE

Anthus spinoletta (Linnaeus)	Water Pipit	B

BOMBYCILLIDAE

Bombycilla garrulus (Linnaeus)	Bohemian Waxwing	(B)

PARULIDAE

Dendroica coronata auduboni (Townsend)	Aubudon's Warbler	S
D. c. coronata (Linnaeus)	Myrtle Warbler	S
Wilsonia pusilla (Wilson)	Wilson's Warbler	S

FRINGILLIDAE

Calcarius lapponicus (Linnaeus)	Lapland Longspur	m
Junco hyemalis hyemalis (Linnaeus)	Slate-colored Junco	S
J. hyemalis oreganus (Townsend)	Oregon Junco	S
Leucosticte tephrocotis (Swainson)	Gray-crowned Rosy Finch	B
Loxia curvirostra Linnaeus	Red Crossbill	S
Passerculus sandwichensis (Gmelin)	Savannah Sparrow	B
Passerella iliaca (Merrem)	Fox Sparrow	B
Pinicola enucleator (Linnaeus)	Pine Grosbeak	S
Spinus pinus (Wilson)	Pine Siskin	S
Spizella breweri Cassin	Brewer's Sparrow	B
S. passerina (Bechstein)	Chipping Sparrow	S
Zonotrichia atricapilla (Gmelin)	Golden-crowned Sparrow	B
Z. leucophrys (Forster)	White-crowned Sparrow	(B)

B = summer nester
(B)= seen but probably not nesting
S = subalpine, but regularly wandering above timberline
m = migrant
u = status uncertain

MAMMALIA

SORICIDAE

Sorex cinereus cinereus Kerr	Masked shrew	uc
S. vagrans obscurus (Merriam)	Vagrant shrew	uc

OCHOTONIDAE

Ochotona princeps princeps (Richardson)	Pika	C

LEPORIDAE

Lepus americanus columbiensis Rhoads	Varying hare	uc

SCIURIDAE

Citellus (Spermophilus) c. columbianus Ord	Columbian ground squirrel	C
C. lateralis tescorum (Hollister)	Golden-mantled ground squirrel	C
Eutamias minimus borealis (Allen)	Least chipmunk	uc
Marmota caligata oxytona Hollister	Hoary marmot	uc
Tamiasciurus hudsonicus columbiensis Howell	Red squirrel	uc

CRICETIDAE

Clethrionomys gapperi athabascae (Preble)	Red-backed vole	uc
Microtus longicaudus vellerosus Allen	Long-tailed vole	
M. pennsylvanicus drummondii (Aud. & Bach.)	Meadow vole	
M. (Arvicola) r. richardsoni (DeKay)	Water vole	ex
Peromyscus maniculatus borealis Mearns	Deer mouse	ex
Phenacomys intermedius levis Howell	Heather vole	uc
Synaptomys borealis chapmani Allen	Lemming vole	ex

ZAPODIDAE

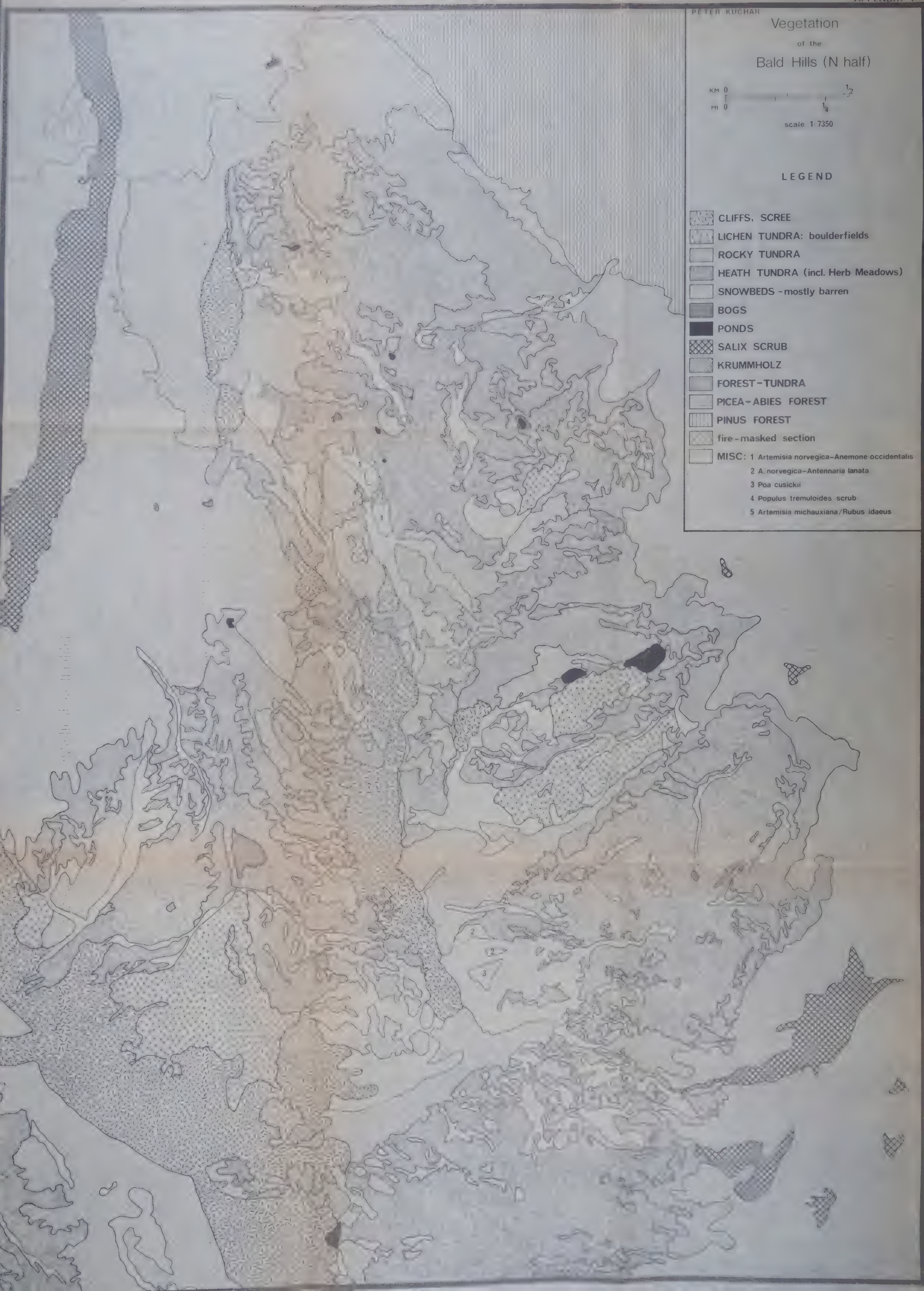
Zapus princeps saltator Allen	Jumping mouse	ex

ERETHIZONTIDAE

Erethizon dorsatum nigrescens Allen	Porcupine	r

CANIDAE		
Canis latrans incolatus Hall	Coyote	r
C. lupus columbianus Goldman	Timber wolf	r
URSIDAE		
Ursus arctos latifrons (Merriam)	Grizzly	uc
MUSTELIDAE		
Gulo luscus luscus (Linnaeus)	Wolverine	uc
Martes americana abietinoides Gray	Marten	uc
M. pennanti columbiana Goldman	Fisher	r
Mustela erminea invicta Hall	Ermine	uc
FELIDAE		
Felis concolor missoulensis Goldman	Cougar	r
Lynx canadensis canadensis Kerr	Canada lynx	
CERVIDAE		
Alces alces andersoni Peterson	Moose	uc
Cervus canadensis nelsoni Bailey	Elk	r
Odocoileus hemionus hemionus (Rafinesque)	Mule deer	C
Rangifer tarandus caribou (Gmelin)	Rocky Mountain caribou	C
BOVIDAE		
Oreamnos americanus missoulae Allen	Mountain goat	uc

C = common
uc = uncommon
r = rare or accidental
ex = expected to occur


PETER KUCHAR
Vegetation
of the
Bald Hills (N half)
KM 0
1/2
MI 0
1/4
scale 1: 7350
LEGEND
CLIFFS, SCREE
LICHEN TUNDRA: boulderfields
ROCKY TUNDRA
HEATH TUNDRA (incl. Herb Meadows)
SNOWBEDS - mostly barren
BOGS
PONDS
SALIX SCRUB
KRUMMHOLZ
FOREST-TUNDRA
PICEA-ABIES FOREST
PINUS FOREST
fire-masked section
MISC: 1 Artemisia norvegica-Anemone occidentalis
2 A. norvegica-Antennaria lanata
3 Poa cusickii
4 Populus tremuloides scrub
5 Artemisia michauxiana/Rubus idaeus

APPENDIX 5. Similarity matrix of Bald Hills vegetation stands and transect segments.

STAND NO.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
30	15	8	11	15	9	13	10	7	7	4	5	7	5	5	2	2	1	2	2	4	4	4	4	8	4	7	2	0	66
29	13	7	9	12	7	8	7	5	5	3	4	4	4	3	2	1	2	2	2	4	5	5	4	8	4	7	1	0	
28	1	0	0	0	0	0	1	0	1	1	1	1	2	2	1	3	13	4	12	3	1	3	17	7	5	1	76		
27	2	2	2	1	1	1	1	1	2	1	2	3	4	2	3	7	14	5	13	5	2	12	22	9	10	2			
26	41	32	16	17	16	11	10	18	38	34	47	52	27	25	22	19	10	12	9	33	16	20	9	21	15				
25	28	12	10	6	5	4	4	8	14	11	10	15	14	16	16	15	22	16	21	37	20	39	43	69					
24	32	12	13	9	6	6	4	12	19	16	10	19	17	15	14	9	22	11	20	36	28	47	38						
23	13	10	7	4	3	4	3	4	9	9	9	13	11	14	10	13	29	13	26	25	18	34							
22	22	14	6	6	3	8	2	11	20	22	15	18	22	16	19	11	31	21	18	50	39								
21	18	10	3	3	2	2	1	6	15	14	10	10	11	12	10	4	14	8	5	24									
20	21	29	17	17	8	6	4	25	33	37	23	34	38	26	33	12	46	24	8										
19	10	12	4	5	5	3	3	6	12	12	15	17	19	31	17	28	47	39											
18	13	13	6	7	5	4	3	16	17	15	13	18	25	45	41	66	28												
17	11	14	11	10	4	4	3	13	15	18	13	19	25	16	20	18													
16	21	13	6	4	7	3	3	7	12	13	23	26	22	37	39														
15	20	27	13	13	10	4	5	22	26	44	30	33	61	62															
14	21	28	12	12	9	6	7	18	27	38	33	38	46																
13	32	39	23	22	20	13	14	45	46	60	45	54																	
12	48	48	32	27	32	17	23	48	60	54	68																		
11	34	36	17	17	20	12	14	41	53	55																			
10	30	48	27	25	21	8	16	49	62																				
9	46	46	31	31	32	13	21	57																					
8	30	43	33	35	27	18	23																						
7	27	29	42	32	47	67																							
6	19	20	34	36	41																								
5	39	35	40	35																									
4	29	35	44																										
3	34	41																											
2	40																												

CASTILLEJA OCCIDENTALIS	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
VERONICA WORMSKJOLDII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gymnomitrium concinnatum & Anthelia juratzkana[4]	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	1	+	+	+	+	.	.	.	.	.	+	2	.	1	+	1	+	+	2	+	1	1	1	.	1	1	2	1	1	.	.	+	+	.	+	1	.	2	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cladonia ecmocyna	.	.	.	.	.	+	.	.	.	.	+	.	.	1	1	1	1	.	1	+	.	.	.	+	+	1	1	1	+	+	.	2	1	1	+	r	1	1	1	1	+	1	2	+	1	.	1	1	1	1	+	+	+	+	+	+	1	+	+	1	+	1	.	+	.	.	+	1	.	1	+	+	+	+	+	+	.	+	+	+	+	+	+	+	.	.	.	.	.	.	.
Peltigera aphthosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	1	.	1	.	.	+	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	2	.	.	.	.	.	.	1	1	1	1	2	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*Cephalozia sp.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
PHYLLODOCE GLANDULIFLORA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	1	2	1	2	1	4	2	3	3	4	4	2	4	1	4	1	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	2	3	2	.	.	.	+	.	.	4	.	.	+	.	1	.	.	.	.	.	.	.	.	.
Lophozia s.l.[5]	+	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	+	.	.	.	+	+	.	+	+	+	.	+	+	+	.	+	+	+	.	+	+	2	+	.	.	.	+	+	1	+	1	.	2	2	.	+	1	1	2	1	+	1	+	.	1	+	1	2	+	1	+	2	1	1	1	1	+	2	+	+	2	1	+	1	+	1	.	.	.	.	.	.
SIBBALDIA PROCUMBENS	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	.	+	+	+	+	+	.	+	+	+	1	+	1	+	+	+	+	.	+	+	+	+	+	+	+	+	+	+	.	.	.	+	.	.	+	+	+	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.
Lepraria neglecta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	1	.	1	+	1	2	1	2	1	1	+	1	1	2	+	+	1	+	1	1	1	+	+	+	1	2	1	.	+	.	.	.	.	+	+	+	1	+	.	+	+	+	+	2	1	+	.	+	1	+	+	1	+	.	.	.	.	.	.	.
CASSIOPE MERTENSIANA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	+	3	4	4	4	4	4	4	4	4	4	3	4	1	1	2	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ANTENNARIA LANATA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1	1	+	1	1	1	1	+	1	+	1	1	1	1	1	+	1	1	1	1	2	2	2	+	.	.	.	.	.	.
CAREX NIGRICANS & C. PYRENAICA[6]	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	1	+	1	1	+	+	+	+	+	+	+	+	+	+	1	+	.	+	.	+	+	+	+	.	+	1	1	1	+	1	+	1	1	1	1	1	1	1	1	1	1	2	3	3	1	.	1	2	4	6	5	6	6	5	5
CAREX SPECTABILIS	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polytrichastrum lyallii & P. alpinum[7]	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	+	+	+	+	.	+	+	+	+	+	+	+	+	+	.	.	+	+	+	.	+	.	+	.	+	+	+	.	+	+	+	.	+	+	+	+	+	+	+	+	.	+	+	+	+	+	+
Drepanocladus uncinatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	1	+	+	+	+	+	+	+	+	1	+	+	+	.	+	.	.	.	+	.	.	.	.	+	.	+	+	.	.	.	+	.	.	+	+	+	+
LUZULA PARVIFLORA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	+	1	.	+	.	.	.	.	+	+	1	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Kiaeria starkei	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	.	1	3	3	4	.	.	1	2	.	2	2	3	3	3	2	3	2	3	1	2	4	2	2	3	3	2	3	.	1	.	.	.	.
Solorina crocea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.	.	.	.	+	.	+	.	.	+	.	+	2	2	.	1	.	+	+	.	+	+	+	+	1	1	+	+	1	+	+	+	1	.	.	.	.	.	.
HIERACIUM GRACILE	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*Polytrichastrum alpinum var. septentrionale	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Lescuraea radicosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.
DESCHAMPSIA ATROPURPUREA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	+	.	.	.	.	+	+	+	.	.	.	.	+	.	+	+	.	+	+	+	+	+	+	+	+	+	+	+	1	1	+	1	.	+	1	.	1	1
Lepraria membranacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
JUNCUS DRUMMONDII	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+	+	.	+	+	+	+	+	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.
LYCOPODIUM ALPINUM	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
LUETKEA PECTINATA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	3	4	2	3	2	2	4	2	2	3	4	3	2	1	2	2	2	4	4	4	3	2	+	.	+	.	.	.
EPILOBIUM ALPINUM	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	+	.	.	.	.	.	.
ERIGERON PEREGRINUS	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Scapania irrigua	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
PEBBLES	+	7	7	7	7	5	7	7	6	3	6	6	6	3	+	2	2	7	3	5	7	7	7	1	+	2	+	+	2	3	+	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MINERAL SOIL	.	+	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	+	.	.	.	2	1	1	5	3	1	1	.	.	.	1	1	.	1	1	2	2	2	1	.	.	.	+	.	1	.	.	.	.	.	.	.	+	1	+	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
LITTER	5	.	.	+	+	4	+	+	+	3	+	+	+	2	3	2	2	+	2	2	.	.	+	3	3	4	4	4	1	4	4	4	4	4	4	4	4	5	4	3	4	4	3	4	5	5	5	4	5	4	4	3	4	4	4	4	5	4	5	5	4	4	4	4	3	4	3	4	4	3	4	5	4	4	4	4	4	4	4	4	3	4	3	4	2	2	4	4	3	3	4
VASCULAR PLANT COVER	3	.	.	.	+	2	+	1	.	2	+	1	1	2	3	2	2	+	1	1	.	+	+	2	3	2	3	3	2	4	5	2	4	4	4	4	3	3	3	4	3	4	3	4	4	4	4	4	4	4	4	4	5	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	5	3	4	4	5	4	3	4	4	4	4	5	5	5	4	6	6	5	6	6	5	5
BRYOPHYTE COVER	1	.	.	+	+	1	.	1	+	1	1	+	1	1	1	1	1	+	1	1	.	.	+	1	1	1	1	2	+	1	2	2	2	3	2	2	2	2	2	2	3	3	2	1	1	2	1	2	1	3	2	4	3	2	2	3	2	4	2	3	3	4	1	2	3	2	3	2	2	3	4	3	3	4	3	3	2	2	4	3	3	3	3	2	4	1	+	+	+	1	1
LICHEN COVER	1	+	+	+	+	2	1	1	2	4	2	2	2	2	3	2	2	+	2	2	+	+	+	4	3	3	3	3	1	2	3	3	3	3	2	3	3	3	3	2	2	3	3	2	2	2	2	2	2	3	3	3	1	1	1	1	3	1	1	1	2	2	2	+	2	2	1	2	1	1	1	1	1	1	2	2	1	1	1	2	1	1	1	1	1						
SUM VASCULAR SPECIES	3				3	2	1	1		4	2	2	3	4	2	2	2	1	2	2		1	2	4	6	6	7	7	4	6	5	8	11	11	8	9	9	8	13	12	10	10	6	8	9	8	10	10	9	10	7	8	8	7	4	5	5	5	7	4	5	4	5	7	7	5	6	5	10	6	5	8	8	8	8	5	7	4	4	10	5	4	6	7	5	2	2	4	1	2	2
SUM BRYOPHYTE SPECIES[8]	7			1	1	4		1	2	5	4	2	2	3	4	3	6	1	3	4			1	3	3	5	6	7	4	5	6	5	6	3	4	4	3	5	6	6	6	5	5	4	6	7	6	6	6	6	6	6	7	6	9	6	9	7	5	5	6	6	4	5	9	3	5	5	4	4	4	5	8	7	3	4	4	4	3	3	4	3	3	3	5	2	1	2	2	3	2
SUM LICHEN SPECIES[8]	10	2	3	4	8	12	6	11	11	14	16	11	11	12	9	13	8	7	9	9	1	1	2	9	9	10	9	10	9	6	9	8	9	8	9	8	7	6	7	7	6	8	5	6	5	5	7	7	7	7	6	8	4	4	5	3	5	6	5	5	4	6	2	3	3	4	5	2	4	3	6	4	6	5	3	6	3	3	6	5	5	4	4	3	2						
SUM ALL SPECIES	20	2	3	5	12	18	7	13	13	23	22	15	16	19	15	18	16	9	14	15	1	1	5	16	18	21	22	24	17	17	20	21	26	22	21	21	19	19	26	25	22	23	16	18	20	20	23	23	22	23	19	22	19	17	18	14	19	18	17	14	15	16	11	15	19	12	16	12	18	13	15	17	22	20	14	15	14	11	13	18	14	11	13	13	12	4	3	6	3	5	4

NOTES: a. Vascular plant species in COURIER CAPITALS, bryophytes in Lower-case, lichens in *Lower-case italics*.
b. Asterisked species are under-represented in analysis. They probably occurred in some other quadrats, but were either too small to be seen in situ or were not distinguished at the time.
c. Rocks greater than 6 cm in diameter occurred only in Quadrats 4 & 13.

[1]Cover scale: +<1% cover, 1=1-5%, 2=6-15%, 3=16-25%, 4=26-50%, 5=51-75%, 6=76-95%, 7=ca.100%

[2]Cephaloziella byssacea identified in Quadrat 1, C. rubella in Q25,28, and C. sp. in Q24,25,28,52,55.

[3]Pohlia cruda recognized in the range Q29-85, Bryum spp. in Q10-91.

[4]Gymnomitrium concinnatum much the more abundant of the two.

[5]Includes Barbilophozia hatcheri, Lophozia spp.

[6]Carex pyrenaica was not recognized until field studies were over. It seems to have been more abundant in the earlier quadrats.

[7]Polytrichastrum lyallii recognized in Q42-91, P. alpinum in Q49-64. Determinations of sterile specimens of the two species are difficult, and misidentifications are possible.

[8]Excludes asterisked species, which would exaggerate species totals of certain quadrats.

APPENDIX 6. Cover estimates of all lichen, bryophyte and vascular plant species in a transect from *Dryas octopetala*/lichen tundra to *Carex nigricans* snowbed.

QUADRAT NUMBER	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–91
**Caloplaca cf. jungermanniae*	+	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
TRISETUM SPICATUM	+	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Dicranum acutifolium	+	+	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Lecidea sp.	+ . + + + . + + . +	+ + ...	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
**Cornicularia aculeata*	+ . . . . +	+	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Rhytidium rugosum	1 . . . . + ...	. . . . . . + . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Mnium blyttii	. . . . . + . . . +	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Hypogymnia intestiniformis	. . . + + + + 1 2 1	2 2 1	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Cetraria commixta	+ . . . + . . 1 + 3	+ + 1 . . . . + . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Umbilicaria hyperborea	. . . . + .	+	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Rhizocarpon geographicum	+ + + + + + + + + +	+ + + + . + . + . .	. . + ...	. 1	. . . .	. . . .	. . . .	. . . .	. . . .
Cetraria tilesii	. . . . . + + + + +	+ + . + . + . + . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Lecanora polytropa	+ + + + + . . + + +	+ + + + . + . + . .	+ + + ...	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Alectoria nigricans + A. ochroleuca	. . . . . + + + + +	+ + + + + + 1 . + +	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
**Lecanora cf. verrucosa*	. . . . +	. + . . . 1	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
POA SP.	. . . .	+ + + + ... + .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Tortula ruralis	. . . . +	. . . . + . 1 . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Alectoria pubescens	. . . . +	. . . . +	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Thamnolia subuliformis	+ . . . + + . + + +	+ + + + + + + + + +	. . . + + + + + + +	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
**Rinodina sp.*	. . . . +	. . . .	. . . + ...	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Rhacomitrium lanuginosum	+ . . . . + +	1 + + + + + + . + +	. . + . . + . . . +	+ . + ...	. . . .	. . . .	. . . .	. . . .	. . . .
Eurhynchium pulchellum	+	. . . .	. . . . . + . + . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Cetraria cucullata + C. nivalis	+ . . . + + . + + +	. + + + + + + . + +	. . . 1 1 1 1 1 . 1	1 1 1 + + ...	. . . .	. . . .	. . . .	. . . .	. . . .
Lecidea granulosa	. . . .	. + ...	. . . . + . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Psoroma hypnorum	. . . .	. . . . . . + . . +	. . . + ...	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
VACCINIUM VITIS-IDAEA	. . . . + ...	+ 1 1 2 3 2 1 + 1 +	. + + + + . + + + .	+ + + . . . + . . .	. . . .	. . . .	. . . .	. . . .	. . . .
DRYAS OCTOPETALA	3 . . . + 2 . . . 1	. . . 1 2 1 1 . 1 1	. . . 2 2 1 1 1 1 2	+ 1 1 1 3 2	. . . .	. . . .	. . . .	. . . .	. . . .
Cladonia cf. macrophyllodes	. . . .	. . . . . . + . . +	. . . + ...	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
*Tritomaria cf. quinquedentata	. . . .	. . . .	. . . . + ...	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Buellia papillata	. . . .	+ . . + ...	. . . . + . .	. + ...	. + ...	. . . .	. . . .	. . . .	. . . .
*Brachythecium sp.	. . . .	. . . .	. . . . . + ...	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
**Cladonia cornuta*	. . . .	. . . .	. . . . . + ...	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
**Lecanora castanea*	. . . .	. . . .	. . . . . + ...	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Dactylina arctica PD+	 1	+ . + . . + ...	. . . . + + + . . .	+ . + 1 1 + . . + +	. . . .	. . . .	. . . .	. . . .	. . . .
*Anastrophyllum minutum	. . . .	. . . .	. . . . . + . + . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
ANTENNARIA ALPINA	. . . . +	. . . + ...	. . . . + ...	. . + + . . + . + .	. . . .	. . . .	. . . .	. . . .	. . . .
*Cephaloziella spp.[2]	+ . . . . +	. . . .	. . . + + . . + . .	. . . .	. . . .	. + . . + ...	. . . .	. . . .	. . . .
Cladonia uncialis	. . . .	. . . .	. . . . + . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
Plagiothecium denticulatum	. . . .	. . . .	. . . . + . .	. . . .	. . . .	. . . .	. . . .	. . . .	. . . .
SALIX NIVALIS	+ . . . + . + 1 . 1	. . . .	. . . 1 + . . + . 1	2 1 1 + 1 . 2 1 1 +	1 1 2 1 1 + 1 + + .	. . . .	. . . .	. . . .	. . . .
Ochrolechia cf. geminipara	. . . .	. . . .	. . . . 1 2 2 1 + .	+ . + ...	. . . .	. . . .	. . . .	. . . .	. . . .
**Pertusaria dactylina*	. . . . +	. . . .	. . . .	. . . . . . + . . .	. + ...	. . . .	. . . .	. . . .	. . . .
FESTUCA BRACHYPHYLLA	. . . .	. . . .	. . . . . + . + . .	+ + + + ...	. . . .	. . . .	. . . .	. . . .	. . . .
*Ceratodon purpureus	+	. . . .	. . . + . + ...	. . . .	. . . .	. . . .	. . . .	. . + ...	. . . .
CAMPANULA LASIOCARPA	. . . . . + ...	. . . .	. . + + + + + + . +	. . + + . + . + . +	+ . . . + . . + + .	. . . .	. . . .	. . . .	. . . .
Cladina mitis	1 . . . . + 1 + + +	+ + + 1 2 1 1 + 1 1	. . . + 1 1 1 + + +	1 1 2 1 1 1 1 + 1 1	+ 2 1 + 1 1 1 1 1 1	1 + + . 1 . 1 + . .	. . . . + .	. . . .	. . . .
Polytrichum piliferum	+ . . + + + . 1 1 1	1 + + 1 1 1 1 + 1 +	. . . 1 + + + + + +	+ 1 1 + + 1 1 + 1 +	+ . . . + + . . + +	+ . + . + . + . + +	. . . .	+ + + + . + ...	. . . .
HIEROCHLOE ALPINA	. . . .	. . + ...	. . . . . . + . . .	. . . .	. . . . . . + . + .	. . . .	. . . .	. . . .	. . . .
CASSIOPE TETRAGONA	. . . .	. . . .	. . . . 2 1 3 3 2 4	5 1 3 3 1 3 2 1 2 2	2 . . + . . . 2 . .	. . . .	. . . .	. . . .	. . . .
SILENE ACAULIS	. . . .	. . . .	 1	. . . . + .	. . . .	. . . .	. . . .	. . . .	. . . .
Stereocaulon alpinum	+ . . . + ... +	+ + + + + 1 1 + 1 1	. . . 4 2 1 + 1 + +	1 + + + + 1 + . . +	+ 1 . + . . . + + 1	+ + . . + . . + . .	. + ... + .	. . . . . + . + + .	. . . .
Paraleucobryum enerve	+	. . . .	. . . . + . .	. . . .	. + . . . + ...	. . . . . . + . . .	. . . .	. . . .	. . . .
Peltigera malacea + P. spuria	+ . . . . + ...	+ . . . + + . . + +	. . . + . + ...	. . + + + . 1 + + .	. + . . . + . . + .	. . . . + . +	+ . . . . . + . + .	. . . .	. . . .
POTENTILLA DIVERSIFOLIA	. . . .	. . . .	. . . . . . + . . .	. . . . + .	. + ...	. . . .	. . . .	. . . .	. . . .
LUZULA SPICATA	. . . .	. . . .	. . . . + + +	. . . . . . + . . .	. . . 1 1 + ...	. . . .	. . . .	. . . .	. . . .
ARTEMISIA NORVEGICA	. . . .	. . . .	. . . . . . + . . .	. + + 1 . . + + . +	. + . . + . + . . +	. + ...	. . . .	. . . .	. . . .
GENTIANA GLAUCA	. . . .	. . . .	. . . . . + ...	. + + + + . . . + .	. . . .	. . . .	. . . .	. . . .	. . . .
PEDICULARIS ARCTICA	. . . .	. . . .	. . . .	. . . . +	. . . .	. . . .	. . . .	. . . .	. . . .
AGROSTIS VARIABILIS	. . . .	. . . .	. . . .	. . . . + +	+ + ...	. . . .	. . . .	. . . .	. . . .
Physconia muscigena	. . . .	. . . .	. . . .	. . . .	. + ...	. . . .	. . . .	. . . .	. . . .
Dicranum scoparium	+ . . . . + ...	. . . . + + + . + 1	. . . 1 + 1 1 1 + +	+ 2 1 3 2 1 2 1 1 2	+ 3 2 1 1 2 + + 1 2	1 1 1 + 1 2 1 2 1 .	. . 1 + 1 . 2 1 . +	. + + 1 . . + . . .	. . . .
Cetraria ericetorum + C. islandica	+ . . . + + . . + .	. . . + + + . . + .	. . . + + + + 1 + +	1 . . + 1 1 + + 1 1	+ + + + + + + + 1 +	1 + . + . . + + + +	1 + . + 1 1 + . . +	1 + + 1 . + + . . +	+ . . . .
SALIX ARCTICA	. . . .	. . . .	. . . . . + ...	. + + 1 1 1 . 1 + +	1 1 1 + + 1 + + + +	+ + + + + 1 1 + + .	. . . .	. . . .	. . . .
Conostomum tetragonum	. . . .	. . . .	. . . . . . + . . .	. . 1 + + + . 1 + +	+ + + + + + + + + +	+ + + + + . + + . .	. . . .	. . . .	. . . .

APPENDIX 7. Abundance trends of dominant cryptogams and vascular plants in a transect[1] from xeric to mesic *Dryas*-dominated tundra.

TRANSECT SEGMENT[2]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
VASCULAR PLANTS																						
Salix nivalis	2	2		1	1	5		+			1	2	3	11	11	5	5	6	1	7	2	15
Dryas octopetala	10	14	15	5	3		5	10	10	5	10	13		2	17	22	29	12	13	31	13	29
Antennaria alpina	1	+												2	1	+	1	+		1	+	2
Luzula spicata		+								+	+			1	1	+	+	1	+	1	1	
Festuca brachyphylla	1	+	+	+		1	+							+	2	+	1	2	3	+	1	1
Arenaria obtusiloba			1				1	+				1		1	2	1	2	1	1	+		+
Gentiana glauca															+	1	4	1		3		3
Salix arctica		1												3				1		3		
LICHENS																						
Umbilicaria spp. & *Cetraria* spp.	+		1	5	4	2			1		1		2									
Sax. crustose spp.	+	+	1	+	1	1	1	1	1	1	1	1	1	1	+		1	+	+	+	+	+
Peltigera spp.	+	1	+								1			+		4	1	+		2		
Cladonia coccifera & *C. pocillum*	2	1	2	+				+	+			+	+	+		1	+	1	+	+	+	+
Cladina mitis (& *Dactylina arctica*)	1	2	2	+	+	+	+	1	1	+	+	2	+	2	+	3	2	1	2	2	1	3
Cetraria spp.	5	5	12	1	1	+	1	4	8	4	5	5	1	3	8	9	6	5	6	9	8	15
Stereocaulon alpinum	5	8	5	4	1		4	4	8	1	2	5	+	9	8	5	5	2	2	5	5	15
Lepraria neglecta & *Lecidea granulosa*	1	1	+	1		+			+	+	+	+	+	19	18	12	3	8	4	2	2	9
SUM VASCULAR COVER	16	22	19	9	5	6	6	11	10	5	11	15	3	20	35	37	47	26	20	49	18	57
SUM BRYOPHYTE COVER	5	2	5	5	+	4		+	5	1	+	4	+	33	4	2	3	9	1	9	8	9
SUM LICHEN COVER	15	10	14	10	6	2	4	4	9	4	7	5	3	28	26	30	16	14	13	15	16	35
CONGLOM. PEBBLES	2		2	1	5	2		5		4	1	4	1				1	1	2			
SHALE PEBBLES	41	26	41	87	83	77	81	66	58	75	71	33	93	5	5	+	3	15	44	17	54	2
SOIL	8	1	2	+	+	+	+	1	+	1	2	2	2	1	1	2	5	20	18	3	6	3
LITTER	29	41	33	5	8	10	10	16	19	10	17	28	1	63	56	63	63	27	24	51	23	74

[1] Entails transect segments 10-19 of Table 21.

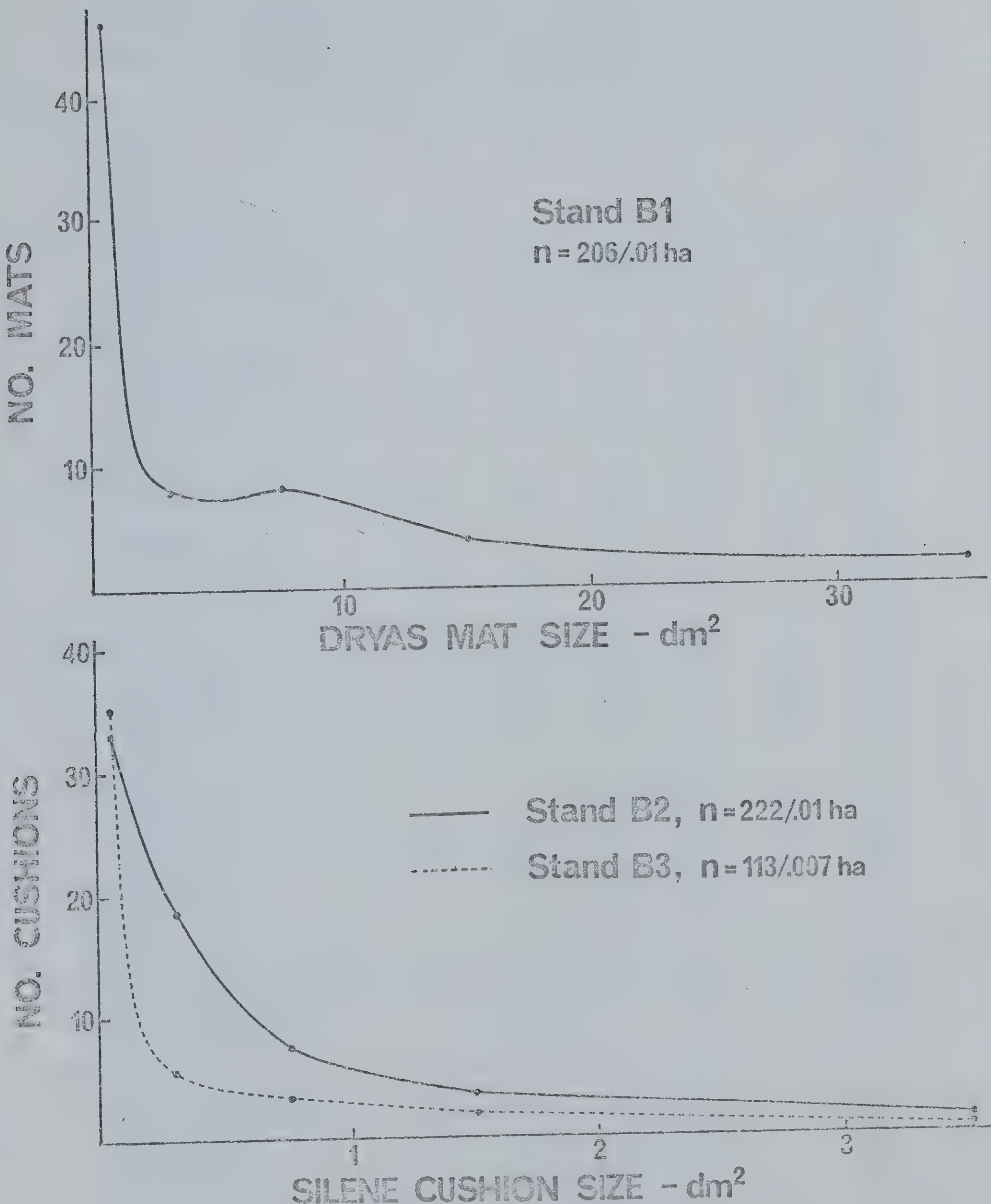
[2] Values represent mean % cover in 2 pairs of 25x25 cm quadrats, each pair at 5 m intervals.

APPENDIX 8. Numbers of occurrences of vascular and cryptogamic plant species within and outside of *Silene acaulis* cushions in a 7x10 m area of cushion-rosette tundra.

ZONE[1]	A	B	C	D	TOTAL
VASCULAR PLANTS					
Arenaria obtusiloba			5		5
Artemisia norvegica	1				1
Carex phaeocephala	2		1		3
Draba cf. *incerta*	9		13		22
Festuca brachyphylla	8	2	1		11
Luzula spicata	1		1		2
Poa arctica	3				3
Poa ?lettermanii	22		1		23
Potentilla diversifolia			7		7
Potentilla ?hyparctica	5		1		6
SUM	51	2	30	0	83
BRYOPHYTES					
Barbilophozia hatcheri	1	1		1	3
Bryum sp.	7	1			8
Ceratodon purpureus	1	1			2
Dicranum sp.	1				1
Hypnum revolutum	7	6		3	16
Paraleucobryum enerve	2				2
Polytrichum ?juniperinum	7	1	1	2	11
Polytrichum piliferum	2	1	1	4	8
Rhacomitrium canescens	5	2		7	14
Rhytidium rugosum	1	1			2
Tortula ruralis	9	3		6	18
SUM	43	17	2	23	85
LICHENS					
Buellia papillata[2]	5				5
Caloplaca jungermanniae & *C. stillicidiorum*	15	1		3	19
Candelariella sp.		1			1
Cetraria cucullata	2	1		3	6
Cetraria cf. *ericetorum*	2	3		4	9
Cetraria tilesii	1				1
Cladonia cf. *ecmocyna*	2	1		1	4
Cladonia coccifera	2	1			3
Dactylina ramulosa	2				2
Ochrolechia sp.	4				4
Peltigera rufescens & *P. spuria*	5	6		5	16
Psoroma hypnorum		1			1
Stereocaulon alpinum	3	4	1	4	12
SUM	39	19	1	20	79
SUM ALL SPECIES	133	38	33	43	247

[1]A = centrally on cushion
B = medially on cushion & at edge
C = unassociated with host plants
D = with host species other than *Silene*

[2]Also possibly *Lecanora castanea*, *Rinodina* sp.



APPENDIX 9. Relationship between size and density of *Dryas octopetala* and *Silene acaulis* populations.

APPENDIX 10. Numbers of arthropods caught in pitfall traps in the Bald Hills through the 1970 season.

	6-12 July	12-24 July	24 July-5 Aug	5-19 Aug	19 Aug-1 Sept	1-15 Sept	TOTAL
DIPLOPODA	1	6	12	31	38	30	118
CHILOPODA		1		2			3
COLLEMBOLA							
Sminthuridae	8	23	1				32
Entomobrya nivalis	85	36	19	27	13	16	196
Isotoma spp.	75	61	102	302	197	276	1013
Morulina nr. *gigantea*		11	27	76	91	51	256
Tomocerus flavescens	154	63	89	192	197	95	791
HOMOPTERA							
Empoasca sp.	1	14	12	21	30	12	90
Scleroracus sp.		2	1	18	26	18	65
Psylla americana		3	51	33	277	270	634
Trioza sp.			1	3	3	2	9
Aphididae	25	20	9	13	24	16	107
Pseudococcidae	6	10	3	14	1	7	41
COLEOPTERA							
Nebria intermedia	16	31	25	32	42	18	164
others	34	87	105	113	73	80	492
LEPIDOPTERA							
Noctuidae ad.		2	1	6	4	4	17
lar.	10	37	16	35	24	2	124
Nepticula spp.	2	1		1			4
DIPTERA							
Bradysia spp.	104	278	142	3918	1428	101	5971
Megaselia spp.	32	143	92	77	53	5	402
Mycetophilidae	8	23	24	14	5	3	77
Empididae	2	8	2	1		4	17
Anthomyiidae	78	158	104	59	25	6	430
Tachinidae				1			1
others	18	15	7	8	12	2	62
HYMENOPTERA							
Tenthredinidae			4	15	10	3	32
Braconidae	4	6	2	9	24	4	49
Ichneumonidae	9	14	10	74	20	8	135
Chalcidoidea	1		6	5	1	15	28
Proctotrupoidea	2	2	18	31	22		75
Bombus spp.			6	12	17		35
PHALANGIDA		2	4	20	23	4	53
ACARINA							
Erythraeus sp.	52	168	283	385	326	11	1225
Podothrombium malignum	17	238	228	195	125	47	850
Microtrombidium sp.	19	63	57	21	36	1	197
Parasitoidea			1			2	3
ARANEA							
Gnaphosa spp.		9	4	17	9	1	40
Micaria hesperella	1	21	8	6	2	1	39
Hahnia glacialis	1	20	11	23	3	1	59
Arctosa insignita		11	6	7	11		35
Pardosa spp.	7	31	35	48	38	3	162
Xysticus spp.		17	10	11	14	3	55
Linyphiidae	13	52	54	106	93	78	396
others		1	8	16	5		30

APPENDIX 11. Mean numbers of arthropods per trap, collected in pitfall traps in various plant communities in the Bald Hills, 11 June - 10 Sept 1972.

COMMUNITY	*Dryas octopetala*/lichen (2250 m)				*D. octopetala*/lichen transect (2350 m)				*D. octopetala*/lichen (2590 m)		*Cassiope tetragona*/ *D. octopetala* (2510 m)	*Phyllodoce-Cassiope* (2250 m)	*D. octopetala*/ moss (2320 m)	cushion-rosette (2320 m)
					shale pebbles									
	Dryas mat	bare shale	hollow	*Empetrum* mat	*Dryas* mat	bare shale	river	conglomerate	*Dryas* mat	gravel				
DIPLOPODA						1.0					1.3	2.7		
COLLEMBOLA	130.1	226.0	257.0	103.0	76.1	143.0	106.0	369.3	132.0	61.3	85.3	101.3	17.5	219.0
INSECTA														
Homoptera	1.2	1.0	4.0	1.0	6.7	1.0		2.3		0.7	2.3	27.7		0.3
Coleoptera ad	6.5	9.0	7.0	8.0	1.0	1.3	2.2	3.2	0.5		1.6	6.6	1.0	3.1
lar	0.1	2.0	7.0	2.0	1.9	1.0	0.9	2.2	0.5		0.4	0.8	1.5	0.7
Lepidoptera ad	2.1	3.0	5.0	7.0	0.3	6.0	4.0	19.2	1.0		0.3	0.5		2.3
lar	4.3	8.0	8.0	2.0	3.0	2.0	11.0	7.3	15.8	2.3	4.0	0.2	2.3	14.0
Diptera														
Bra[illegible]ela spp.	987.1	465.0	1749.0	1322.0	88.0	77.0	48.0	422.7	41.0	0.7	15.0	22.7	5.0	19.0
others	76.6	85.0	51.0	75.0	17.1	37.0	16.0	52.0	60.6	5.0	0.6	36.6	28.5	26.2
Hymenoptera	48.5	91.0	10.0	60.0	16.3	31.0	23.0	30.0	12.0	2.6	0.9	16.1	33.0	20.1
PHALANGIDA									0.3		0.3			
ACARINA	197.5	89.0	619.0	220.0	103.3	44.0	33.0	91.2	246.2	6.0	25.6	56.1	246.0	17.3
ARANEA	42.3	130.0	67.0	33.0	78.7	130.0	45.0	83.1	22.7	9.3	1.0	51.4	29.5	29.5